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Choosing Spatial Units for Landscape-Based Management of the Fisheries Protection Program

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Canada

Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

With the 2012 revisions of the federal *Fisheries Act* there is a need to manage the risk to fisheries productivity from anthropogenic activity; however, the scale at which overall productivity should be managed is not clear. In this document, we review how Ecologically Based Management Areas (EBMAs) are developed using both terrestrial and aquatic variables. We present a range of existing EBMA schemes and, for a few, demonstrate their effectiveness at different spatial scales in predicting aquatic variables that are relevant to fisheries production. Last, we present the insights from expert contributions on aspects of developing regional benchmarks of inland fisheries productivity in Canada. We conclude that any EBMA approach for managing Canada's fisheries productivity will almost certainly increase the number of management areas from the existing six regions. From the few studies available, it appears that intermediate scale management areas (i.e. 20,000 km^2) are effective at partitioning variation in important aquatic parameters among regions. Existing classification levels that match this insight are Canadian terrestrial Ecoregions, Ontario's Fisheries Management Zones, British Columbia's Management Areas, and the United States' EPA Level III Ecoregions. We also conclude that there are many ecological models available which allow for fisheries production to be estimated from both broad-scale, top-down approaches and fine-scale, bottom-up approaches. Following recent insight from ecological classification literature, a promising approach for developing EBMAs for use in the Fisheries Protection Program would involve broad-scale parameters that incorporate climatic and geophysical variables as well as at least one of each of the following: terrestrial, aquatic and anthropogenic variables. Once the broad-scale parameters set the foundation of the EBMA, finer scaled variables could also be used to estimate fish production in a range of management scenarios.

Sélection des unités spatiales pour la gestion fondée sur les paysages du Programme de protection des pêches

RÉSUMÉ

En raison des modifications apportées à la *Loi sur les pêches* en 2012, il faut gérer le risque pour la productivité des pêches posé par les activités anthropiques; cependant, l'échelle à laquelle la productivité globale devrait être gérée n'est pas claire. Dans le présent document, nous examinons la façon dont les zones de gestion écologique sont élaborées à l'aide de variables terrestres et aquatiques. Nous présentons différents systèmes existants de zones de gestion écologique, et pour quelques-uns d'entre eux, nous démontrons leur efficacité à différentes échelles spatiales quant à la prévision des variables aquatiques qui touchent la production des pêches. Enfin, nous présentons les notions découlant des contributions d'experts sur les aspects de l'élaboration des points de référence régionaux de la productivité des pêches dans les eaux intérieures au Canada. Nous avons conclu que n'importe quelle approche de zone de gestion écologique pour la gestion de la productivité des pêches du Canada permettra très probablement d'accroître le nombre de zones de gestion des six régions existantes. Selon les quelques études disponibles, il semble que les zones de gestion à échelle intermédiaire (c.-à-d., 20 000 km^2) sont efficaces pour répartir la variation des importants paramètres aquatiques entre les régions. Les niveaux de classification existants qui correspondent à cette notion sont les écorégions terrestres du Canada, les zones de gestion des pêches de l'Ontario, les zones de gestion de la Colombie-Britannique et les écorégions de niveau III de l'Agence EPA des États-Unis. Nous avons également conclu qu'il existe de nombreux modèles écologiques disponibles qui permettent d'estimer la production des pêches au moyen d'approches descendantes à grande échelle et d'approches ascendantes à petite échelle. À la suite d'une récente étude de la documentation sur la classification écologique, une approche prometteuse pour l'élaboration de zones de gestion écologique aux fins d'utilisation dans le Programme de protection des pêches comprendrait des paramètres à grande échelle qui intégreraient des variables climatiques et géophysiques, ainsi qu'au moins l'une de chacune des variables terrestres, aquatiques et anthropiques suivantes. Une fois que les paramètres à grande échelle auront établi le fondement de la zone de gestion écologique, des variables à plus petite échelle pourraient également être utilisées pour estimer la production des poissons dans une gamme de scénarios de gestion.

BACKGROUND LITERATURE REVIEW

STATEMENT OF PURPOSE

The revision of the federal *Fisheries Act* in 2012 created a new and central role for fisheries productivity in the associated Fisheries Protection Program (FPP) policy. As outlined in a summary publication of the science supporting the policy process (Rice et al 2015), from self-assessment to managing serious harm, the risk to fisheries productivity remains the central property being assessed, either directly or indirectly. This revision and new policy represents a significant shift in focus from the previous Fish Habitat Management Program (FHMP), for which the focus of the *Fisheries Act* was the protection of fish habitat from harmful alteration, disruption or destruction. This shift is presented in section 6 of the new act such that the Minister will consider *"the contribution of the relevant fish to the ongoing productivity of commercial, recreational or Aboriginal fisheries"* when deciding whether to authorize human activity or development that will cause *"the death of fish or any permanent alteration to, or destruction of, fish habitat"*. Since the amendment of the Act, the science and policy divisions of Fisheries and Oceans Canada (DFO) through the Canadian Science Advisory Secretariat have been providing technical advice on the implications of the new focus on the FFP including:

- the identification of species and habitats that support commercial, recreational or Aboriginal (CRA) fisheries (Kenchington et al 2012);
- the detailed interpretation of the phrase "ongoing productivity of CRA fisheries" (Randall et al 2012);
- the detailed interpretation of the phrase "contribution of relevant fish to the ongoing productivity of CRA fisheries" (Koops et al 2013);
- a review of productivity-state response curves, which effectively link environmental change to changes in fish traits and fisheries qualities (Koops et al 2013);
- elucidation of a framework to assess fisheries productivity under the FPP (Bradford et al 2013);
- identification of promising ecological indicators for measuring and monitoring fisheries productivity (de Kerckhove 2014);
- advice on how to offset losses to productivity (Loughlin and Clarke 2013, Clarke and Bradford 2013); and,
- how to manage residual impacts to fish and fish habitat (Bradford et al. 2015).

The purpose of this Research Document is to continue to provide advice on the implementation of the revised *Fisheries Act* and the FPP policy. In particular, this report discusses what spatial unit of area would be most appropriate for managing fisheries productivity across Canada's diverse inland fisheries. With the emerging FPP policy, benchmarks of fisheries productivity are a desirable management tool (Randall et al. 2016) and so it is important to determine the area of landscape for which it becomes feasible to characterize a representative level of fish productivity for a region. Under the previous FHMP policy, the management areas for the country were divided along logistically convenient boundaries from a jurisdictional perspective (i.e. provincial and territorial boundaries), but not necessarily from an ecological one (Figure 1). Indeed, the DFO regions largely reflect the historic focus on marine fisheries. For example, from a perspective of fisheries productivity the Central and Arctic Region, which includes all of Ontario, Manitoba, Saskatchewan, Alberta, Northwest Territories and Nunavut, contains one of

the broadest ranges in species richness, annual temperatures and geology in the country, and so managing for a common level of fisheries productivity across this region is not necessarily feasible or warranted. However, even if we could estimate regional productivity, what would we choose as the metric that would define an upper threshold to the management area size, or identify a boundary on a map? We could for example define the threshold such that the co-efficient of variation associated with the regional productivity estimate was low enough that changes to the fisheries could be identified within a suitable management timeline (Jones and Petreman 2012). Alternatively, we could set boundaries such that fish productivity was expected to be relatively even across a region, and significantly different between adjacent regions. There are other ways in which these boundaries could be set, and so the purpose of this report is to explore different schemes of setting the size of spatial units of ecosystem management. We begin by introducing ecologically based management area schemes used in terrestrial and aquatic systems and discuss whether terrestrial schemes are relevant to aquatic communities. Next we present how different spatial scales of management influence the ability to monitor or predict ecosystem change in lakes and rivers. Last, we present solicited contributions from experts on ecological drivers of fisheries productivity, and how those drivers might inform us on the appropriate size of management areas in Canada.

Figure 1. The six administrative regions of Fisheries and Oceans Canada.

SETTING ECOLOGICALLY BASED MANAGEMENT AREAS (EBMA)

The process of classifying or mapping of ecological factors is effectively a reflection of the state of science on a particular landscape feature or the relationships among features at any one time. Ideally, any classification would address well known empirical relationships between the ecological drivers of change and characteristics of landscapes, while providing an output or framework that could directly address a particular management issues (Young et al. 2002, Soranno et al. 2010, Melles et al. 2012). For example, under the FPP the classification system would ideally allow management decisions to be based on the risk that a change on the landscape would lead to a significant reduction in fisheries productivity. For this, the relationship between the landscape features and fish productivity would need to be known at both a local level at the site of the impact, and at the scale of the management area to put the magnitude of

the risk in a proper context. However, these relationships are often not known and therefore, the confidence that the scientific community has in a landscape variable to reflect a management priority is directly tied to the applied value of a classification system. With this in mind, Melles and colleagues (2013) present four general principles that classifications of ecological features across a landscape often represent:

1. Organization of known information such that inductive generalizations about the components of the ecosystem can be made (Portt et al. 1989);
2. Provision of an appropriate spatial context for monitoring, management, inventories and reporting (also termed an "economy of memory" by Sokal (1974));
3. Acknowledgement that new features that might arise over time which require inclusion within the classification structure;
4. The explicit creation of a hypothesis of how ecosystem features interact across the landscape.

These principles may not be successfully achieved for all approaches, but they provide useful goalposts to set the objectives of new classification systems. Typically, the development of ecologically based management areas (EBMAs) follows three general approaches. The first is a hierarchical approach in which finer scaled features (i.e. site specific measurements) are nested within large scale features (i.e. climate, geology). This approach leads to EBMAs that are contiguous within a particular area at the highest hierarchical scale and have defined boundaries and unique characteristics. Within these hierarchies, nested levels never overlap on each other or cross upper level boundaries. As such, the development of boundaries at each level involves looking for new environmental variables that can subdivide the existing area. In contrast, a second approach may look at similarities among a particular landscape features (e.g. water depth) or a biotic metric (e.g. species richness) leading to a patchwork of non-contiguous units that are similar. These EBMAs will not necessarily have any prior relationship with a particular place in the landscape, especially if the ecological mechanisms that shape the abiotic features or biotic metrics are not clearly related to a global or regional landscape variable. An applied example of this approach is to group lakes by size classes and apply management rules to each group. This works particularly well for fish species whose life history are influenced more by lake size than geographic location (e.g. Lake Trout, Shuter et al. 1998, Samarasin et al. 2015). A final contrasting method is one in which the subsections of a waterbody (i.e. headwaters vs main stem, or littoral vs pelagic zones) are of interest to management. These EBMAs are dependent on a particular location in space such as the distance from the headwaters, but are non-contiguous such that a patchwork of similar EBMAs will occur across a landscape.

From a management perspective, it often seems logistically convenient (as well as intuitive) to manage one contiguous and well defined territory as one management unit (i.e. the existing DFO administrative regions). This perspective clearly has historical roots in Canada as well, given that land was traditionally delineated as contiguous and well defined parcels spanning different levels of public and private ownership. Given this history, it might seem easiest to choose the first approach and focus all efforts on managing a unique and well defined EBMA. However, setting clear ecological boundaries to define contiguous areas will always be challenging, especially given that even natural breaks (e.g. waterfalls, watershed boundaries, drainage basins) are not always easy to define. For example, different processes shape watersheds within predominantly dry, moist and wet forest types, and therefore, the delineation of watershed boundaries can be difficult to define, if not impossible within low-relief areas. Further, even if natural breaks are clearly delineated, their relevance to the ecology of organisms on either side of the break may not be as clear. For example, it is intuitive that two adjacent headwaters may have similar properties, and thus the boundary created by the highest

points of elevation between the two could have very little ecological relevance. Further, longitudinal changes within a watershed may have a very high ecological relevance but a very fuzzy boundary. If we combine these last two examples, we illustrate a major challenge with creating EBMAs. In watersheds, the headwater tributaries, main-stem river, lakes and wetlands will often share more similarities in environmental features with the same habitat feature in other watersheds than among each other (Kratz et al. 1997, Finn et al. 2011). This example illustrates a general problem with attempting to create distinct boundaries in systems that are inherently complex. In aquatic ecosystems the boundaries that contain water may seem easier to define than in a terrestrial context, however this perception oversimplifies the complexity of branched and dendritic fluvial systems in which lakes or wetlands can occur at any longitudinal spot and have an important influence on biotic features and fisheries productivity. Last, there is little evidence that the management of a contiguous area will be more effective than addressing a patchwork of similar environments (Jenerette et al. 2002). For example, watersheds that run partially through protected areas generally do not demonstrate noticeable improvements in fish biomass or diversity (Adams et al 2015), yet widespread stewardship efforts in headwaters across multiple watersheds can be quite effective conservation initiatives (e.g. the Eastern Brook Trout Joint Venture; http://easternbrooktrout.org/).

In spite of these challenges, any of the three EBMA types mentioned above are increasingly used by regulators and favoured by scientists over jurisdictionally defined management areas in all types of environments. In recognizing that they represent an ecological hypothesis, scientists and managers can determine how much uncertainty is acceptable for certain management priorities and clearly identify assumptions on the relationships between landscape features and the target resource that may be tenuous or outdated. Inherent assumptions to EBMAs include 1) that boundaries between EBMAs represent a significant difference in a variable that is being managed (e.g. fisheries productivity) because the mechanisms that define the boundary (e.g. climate, geology) are homogenous within the EBMA, and 2) that habitats within the EBMA will all respond similarly to management actions (Bailey 1983). Testing these assumptions could be valuable in determining how much confidence is placed in a particular relationship. For example, changes in geology can mirror changes in species distributions because both of these variables were influenced by the retreat of glaciers. However, species distributions are also influence by contemporary factors including habitat fragmentation, species invasions and competitive exclusion. In testing the assumption by contrasting the additional mechanisms with the one that defines the EBMA, a level of certainty in the EBMA classification can be achieved. The previous example is admittedly an ideal situation. Management regions are often subjective (Melles et al 2014), rarely based on a mechanistic understanding of ecological processes (Hawkins et al. 2000, Young et al. 2002) and rely on expert opinion of delineations between regional ecosystems (Kleynhans et al. 2005, Higgins et al. 2005). However, with the increasing creation of EBMAs across the globe, it is becoming clear that a mixture of approaches that lead to hierarchical delineations of spaces and non-contiguous classification of habitat that include clear mechanisms between landscape features and biotic metrics can be effective (Wichert et al. 2004, Seelbach et al. 2006). Using this type of method can lead to hierarchical EBMAs in which larger spatial scales have contiguous regions and lower scales are non-contiguous or even overlapping.

Hierarchical classification systems generally assume that mechanisms at the largest scale constrain ecosystem characteristics at finer scales (both temporal and spatial; Frissell et al. 1986). Thus any change in top-down mechanisms (e.g. climate) is expected to shift the nested ecological characteristics in a corresponding manner whereas bottom-up changes will have very little effect (Frissell et al. 1986, Naiman et al. 1992; but see Melles et al., 2012 for a different view). Using this hierarchical scheme, the broadest levels of classification are determined mostly by climate related variables such as annual averages in temperature, evapo-transpiration

and precipitation, as well as by regional weather patterns including the lengths of seasons or temperature extremes. The influence of geology and topography is typically found to act in concert with climate at a lower level within the hierarchy (albeit remaining at a fairly large spatial scale). At finer spatial scales (i.e. within much more local spatial extents) biotic interactions become more important in determining ecological patterns.

Melles and colleagues (2013) conducted an extensive review of Aquatic Ecosystem Classification schemes in preparation for classifying lotic environments within Ontario and found that top-down mechanisms were the most prevalent. Out of a review of 37 classification scheme the three most common justifications for choosing the variables that set boundaries among areas were that the "variables covary with important ecological attributes or controlling factors", they were "easily quantifiable / mappable" and they were "representative of catchment-scale hydrological or local scale geomorphic processes". Among 81 studies over half of the classification schemes included aspects of Geology, Hydrology and Morphology / Topography, with Climate being the next most common in just under half of the studies. Two-thirds of these studies involved multiple levels of a hierarchical scheme and of those, another two thirds were driven by top-down processes and thus classified particular areas of the landscape. Schemes which involved both top-down and bottom up approaches with place-independent variables were found in the one-quarter of the studies. However, in the non-hierarchical studies, all but one scheme included place independent variables. While top-down mechanisms were the most prevalent in the review, Melles et al. (2013) point out that changes within local scales, especially those brought on by biotic interactions, may not only be a response variable to upper levels within the hierarchy, but also a transformative ecosystem process variables in their own right. As an example taken from Feist and colleagues (2010), riparian conditions can influence the availability of coarse organic matter which influences sediment aggradation and can ultimately influence the geomorphology of the watershed. Another more common example is the influence of beaver dams on watersheds.

Historically, EBMAs have been generally nested, hierarchical systems for which the largest spatial scales are defined by climatic and geological variables, and the finer scales by clusters of similar organisms. For example, Crowley (1967) developed a four level classification scheme including (from largest to finest scales): domains, divisions, provinces and sections. Crowley's scheme is not unlike the common schemes found today including:

- Canadian terrestrial classification (from largest to finest scales): Ecozone, Ecoprovince, Ecoregion and Ecodistricts (see Table 1 for sizes and numbers in Canada, Figure 2; Ecological Stratification Working Group 1995, Ricketts et al. 1999)
- ECOMAP's hierarchy: Ecoregions (26,000 – 2,600,000 km^2), Subregions (26 – 2600 km^2), Landscapes (4 - 40 km^2) and Land Units (0.04 – 0.4 km^2) (Cleland et al. 1997, ECOMAP 2007)
- The Nature Conservancy's aquatic classification: Zoogeographic Units (10,000 – 100,000 km^2), Ecological Drainage Units (1,000 – 10,000 km^2), Aquatic Ecological Systems (10 – 1,000 km^2), Macrohabitats (1 – 10 km long).
- Mandrak's (1999) aquatic classification in Ontario: ecozones, ecoprovinces and ecoregions based on a correspondence between aquatic eco-regional groupings and fish faunal regions.
- The Commission for Environmental Co-operation and the U.S. Environmental Protection Agency's ecoregions based on a refinement of Omernik (1987): Level I (15 in North America), Level II (50 in North America), Level III (182 in North America) and Level IV (incompletely mapped) (see Figure 3).

- Perrin and Blyth's (1998) classification in British Columbia: ecoprovinces (8 separated by geoclimatic factors), ecoregions (45 separated by macroclimatic, geolithic and geomorphic factors) and watershed groups (245 separated by site level factors such as TDS, pH and alkalinity.
- The Nature Conservancy Canada's EAU BC (Ciruna et al. 2007): ecoregions (place-dependent and contiguous) ecological drainage units (place-dependent and contiguous) and river/lake ecosystems (place independent with 11 river ecosystem types, 23 river ecosystem sub-types and 9 lake types).

Table 1. Eco-classification systems in Canada.

Terrestrial

Eco-classification	Range in Area	Map Scale	Number in Canada	Relevant Reference
Continental Ecozones	500,000 - 50,000,000 km^2	World Map	1	N/A
Ecozone	150,000 - 2,000,000 km^2	1:7,500,000	15	Ricketts et al. 1999
Ecoprovinces	50,000 - 500,000 km^2	1:2,000,000	53	Ricketts et al. 1999
Ecoregions	25,000 - 500,000 km^2	1:500,000	194	ECOMAP 2007
Biogeoclimatic	25 - 2,500 km^2	1:100,000	N/A	Perrin and Blyth 1998
Ecodistricts, Land Resources Areas	5 - 50 km^2	1:20,000	1021	Ricketts et al. 1999
Land Unit	0.5 - 5 km^2	1:20,000	N/A	ECOMAP 2007

Aquatic

Eco-classification	Range in Area	Map Scale	Number in Canada	Relevant Reference
Marine Ecozones	25,000 - 2,000,000 km^2	1:7,500,000	5	Wilkinson et al. 2009
Freshwater Ecozones	250,000 - 1,000,000 km^2	1:7,500,000	18	Abell et al. 2008

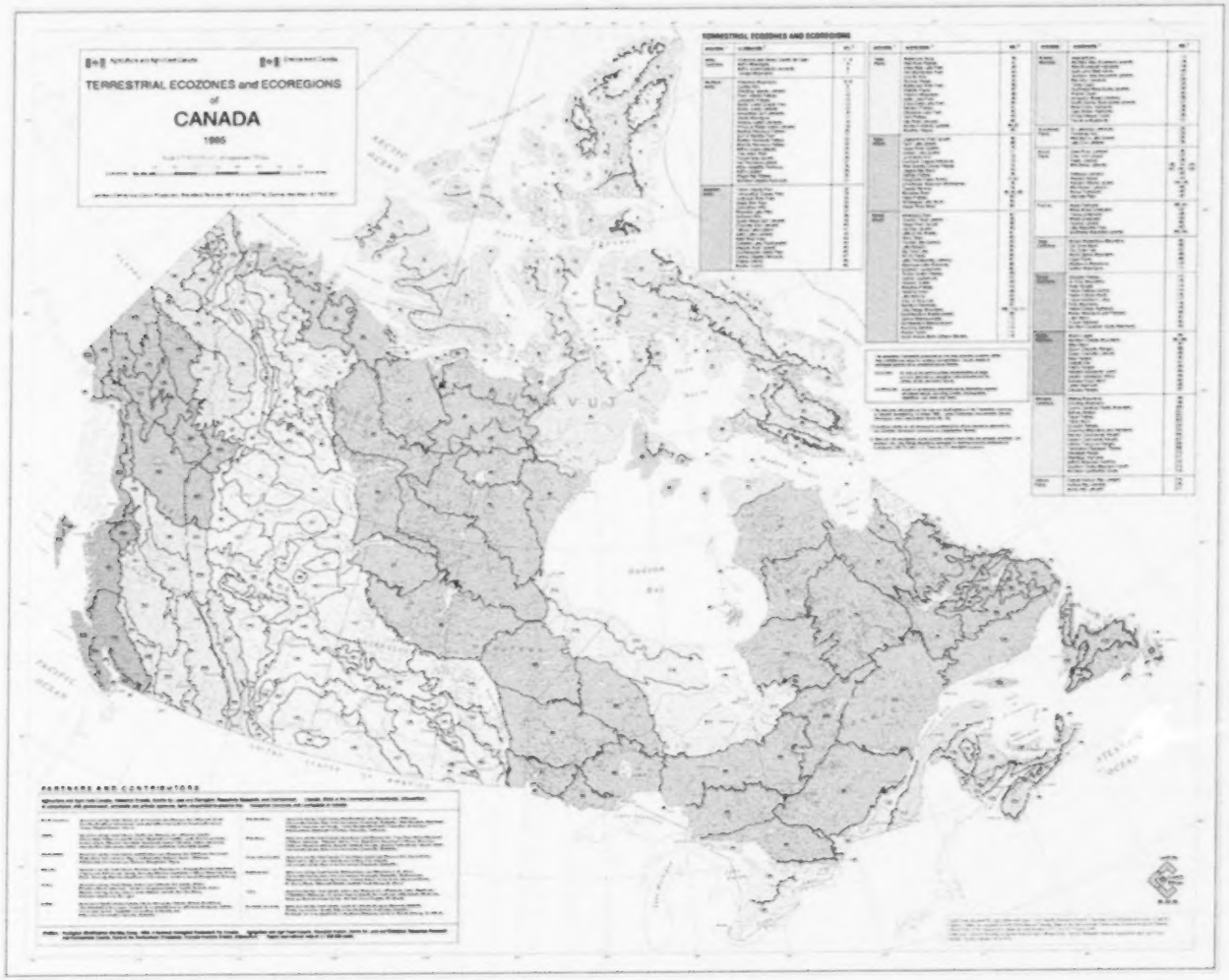


Figure 2. Canada's terrestrial ecozones and ecoregions (Source: Ecological Stratification Working Group 1995).

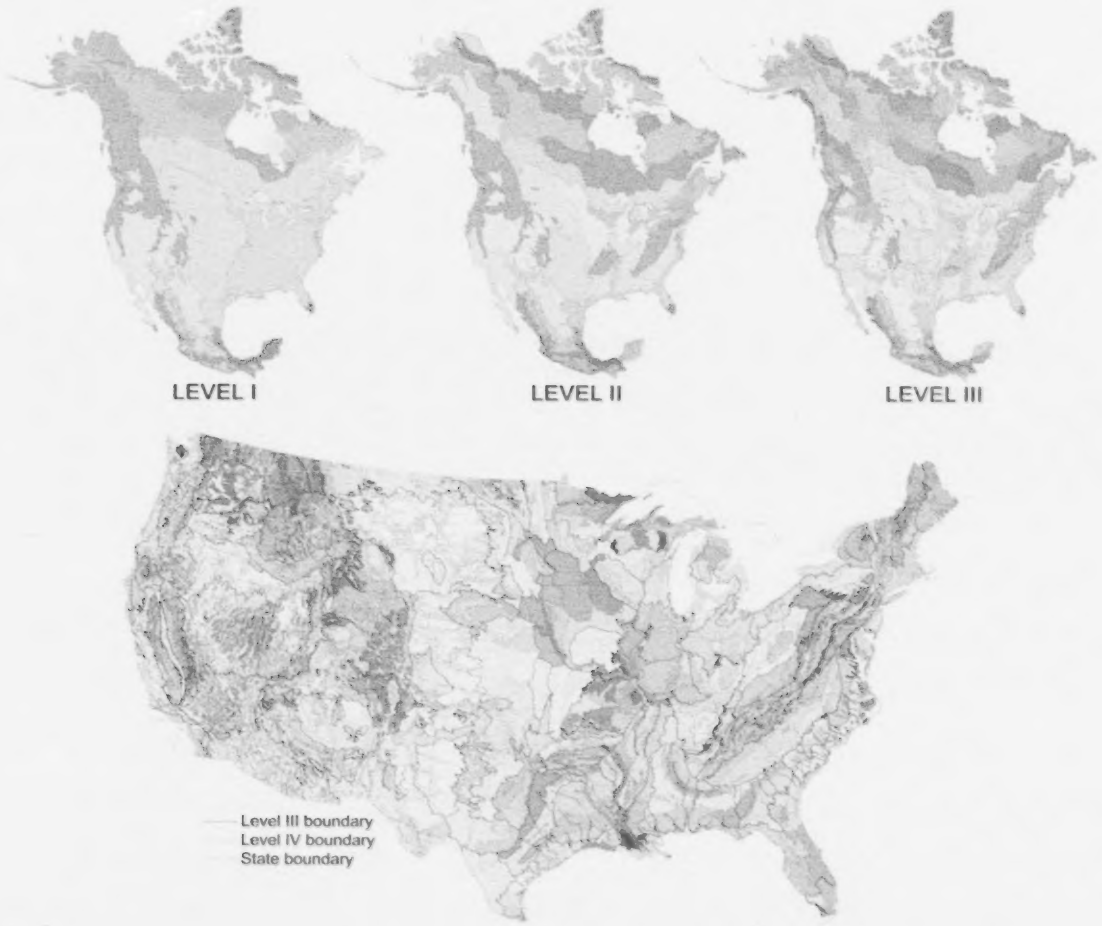


Figure 3. CEC and EPA Level I – III ecosystem classifications for North America (top row) and Level IV for the United States of America (Source: Omernik and Griffith 2014).

AQUATIC CLASSIFICATIONS SCHEMES

The classification schemes listed in Table 1 and depicted in Figures 2 and 3 are predominantly based on large scale climatic and geological variables and fine-scaled distributions of terrestrial species and landscape features. However, the same methods have been applied using large scale drainage patterns and fine-scale aquatic species or watershed features to generate aquatic classification schemes. We present the freshwater ecozones mapped by Abell and colleagues (2008) as well as the insights of two extensive reviews, one on lakes (Leach & Herron 1992) and the other primarily on streams (Melles et al. 2013).

Broad freshwater ecoregions were mapped by Abell and colleagues (2008) using fish biogeography and watershed boundaries (Figure 4). This initiative defined an ecoregion as "a large area encompassing one or more freshwater systems with a distinct assemblage of natural freshwater communities and species". While neighbouring ecoregions have dissimilar assemblages of species, the boundaries are not necessarily determined by the turnover of species ranges, but are instead broader patterns. Different approaches were used to delineate the zones in different parts of the planet, and, in Canada, a cluster analysis was conducted on fish occurrence records in the secondary watersheds within the country's nine primary watersheds. The process for mapping the regions was implicitly hierarchical with the assumption that since watersheds were nested, the fish communities in secondary watersheds would be constrained by the fish assemblages in the primary watersheds, which were shaped through glaciation. This process identified roughly 18 ecozones in Canada. In comparison to the 15 Canadian terrestrial ecozones, the freshwater ecozones are slightly more evenly distributed in size and share similar boundaries.

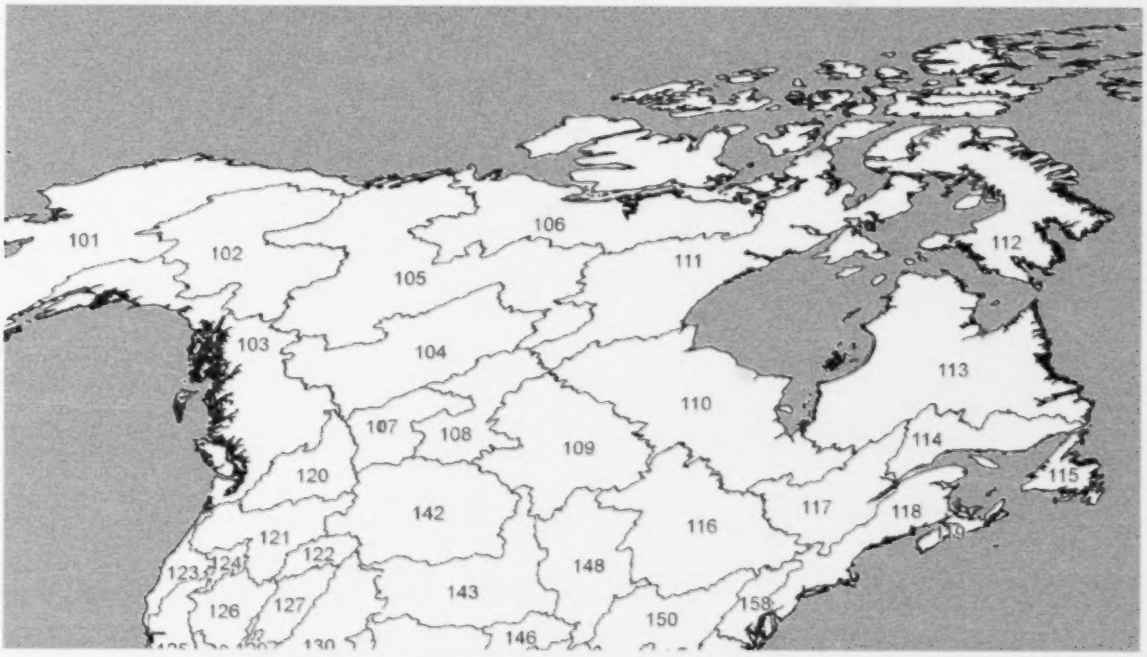


Figure 4. The freshwater ecoregions found in Canada. Note that the descriptions can be found in the source (Abell et al. 2008) and this figure has been modified from its original presentation.

In their review Melles et al. (2013) present a wide range of stream habitat classification studies, and demonstrate that abiotic attributes that have the potential to determine the

presence/absence of species are used much more often than the actual species distributions. This is in contrast to the freshwater ecozones presented above, in which species distributions were the primary variable that was used for clustering groups among watersheds (Abell et al. 2008). Melles et al. (2013) go on to present four main types of abiotic classifications:

1. Geoclimatic: the primary use of climate, physiography and surficial geology
2. Geomorphic: the use of elements of channel morphology including valley and reach slopes, substrates, and pool / riffle frequencies
3. Hydrologic: the primary use of stream flow
4. Chemical: the use of water quality parameters including conductivity, turbidity and temperature

Leach and Heron (1992) reviewed approximately 140 studies on lake classification systems, of which the majority were related to lake trophic status and its response to eutrophication. The authors suggested that a hierarchical classification scheme with global, regional and infra-regional levels (i.e. within regions) and informed by temperature, area, nutrient levels and lake morphometry would be the most appropriate approach. In their review, they found five basic types of lake classification:

1. Geospatial: the use of often place dependent variables including lake origin, lake shape and its regional location
2. Physical: the use of water temperatures, lake stratification and water clarity
3. Chemical: the use of water quality parameters including nutrients and acidity
4. Trophic: the nutrient status including oligotrophic, mesotrophic and eutrophic
5. Biotic: the fish assemblage and fish habitat

From these three examples it is clear that aquatic schemes can be created using very different sources of data, and as such, the management implications of each type of approach can be surmised. For example, the use of species distributions in the freshwater ecozones (Abell et al. 2008) and in the 5th basic type of lake classification system (i.e. "Biotic"; Leach & Heron 1992) would create spatial units that could be used to effectively preserve biodiversity across Canada. However, these management units may not be as effective at managing fisheries productivity as there is no indication from this scheme that the boundaries in species distributions are similar to natural breaks in fish biomass and production. On the other hand, chemical and trophic drivers of aquatic classification schemes could indeed correlate well with fisheries productivity, even though they are typically developed to manage impacts to water quality (e.g. eutrophication).

USE OF TERRESTRIAL CLASSIFICATIONS IN EXPLAINING AQUATIC ECOLOGICAL INDICATORS

Most classification schemes are based on predominantly atmospheric or terrestrial mechanisms, and don't necessarily incorporate aquatic variables. However, in many schemes, the mechanisms at each level are neither strictly terrestrial or aquatic (e.g. climate, geology, physiography) nor include any biotic variables that would focus on one or the other. In a review of classification scheme conducted by Lotspeich and Platts (1982) they explicitly excluded aquatic studies with the reasoning that their distinction from one another is artificial because "land and water function as one unit". However, as demonstrated above, aquatic classification schemes are neither rare (Portt et al. 1989, Uhlig & Baker 1994, Mandrak 1999, Hawkins et al. 2000, Abell et al. 2008) nor recent (Carpenter 1928), so there has been ample opportunity to compare aquatic and terrestrial classification schemes. However, while we present the insights from some of these comparisons, Omernik and Bailey (1997) cautioned that comparing the distributions or abundances of any biotic resource to ecoregion land classifications is an inherently flawed approach because the comparison is occurring across hierarchical levels.

Warry and Hanau (1993) found that terrestrial classification schemes were well suited to explain variation water chemistry, yet they admitted that a more thorough statistical analysis was needed. Mandrak (1998, 1999) developed an aquatic classification system and compared it along with other aquatic spatial delineations and ecological indicators to terrestrial ecozones and ecoregions in Ontario. First, he found weak areal correspondence between terrestrial ecoregions and tertiary watersheds or fish faunal regions. However, since the broadest level within his aquatic classification system was driven mainly by geology and climate, his five aquatic ecozones corresponded well with the three terrestrial ecozones in Ontario. Hawkins and Norris (2000) chaired a symposium testing these same types of correspondences by measuring the difference between mean within-class and mean between-class similarity of aquatic biotic variability within terrestrial and aquatic classification regions. Generally, the symposium concluded that terrestrial classification schemes had a "limited application in aquatic bio-assessments" (Hawkins et al. 2000b), even though all of the classification schemes were able to explain more variation in aquatic ecological indicators than by chance alone. An important insight from the symposium was that landscapes with a highly varied topography were where the best correspondences between terrestrial classification schemes and aquatic ecological indicators were found. Wichert and colleagues (2004) found similarly to Mandrak (1999) that terrestrial regions did not correspond well to fish faunal zones. Last, Chu and Jones (2010) found that water temperatures were much more variable within than between terrestrial eco-districts.

With Omernik and Bailey's (1997) caveat in mind, it appears from these studies that terrestrial classification schemes are able to show some weak correspondence with aquatic variables, but on the whole they do not provide any substantial statistical power in delineating aquatic groups across boundaries, except perhaps at the highest levels of hierarchical schemes. This low power can be explained by a few main reasons. First, one of the greatest sources of variation within watersheds is the longitudinal patterns found in rivers in both abiotic parameters (i.e. water quality) and biotic indicators (fish abundance and richness), as well as the non-intuitive physical and ecological patterns shaped by uni-directional flow. These processes are not found in terrestrial systems (except perhaps up mountain ranges) and so will not be captured in terrestrial classification schemes. Second, difference in aquatic parameters such as water quality, are unlikely to be represented well by the common set of variables that shape terrestrial classification schemes. For example, the presence or absence of lakes and/or wetlands within watersheds can lead to very different ecological conditions, even within similar aquatic regions (Jones 2010). While upper levels of a hierarchical system may distinguish some of these aquatic parameters (e.g. regions with high numbers of lakes such as the Canadian shield), they won't be able to account for fine-scale variability in other important physical variables such as stream temperature or land-cover. Last, in north temperate environments, there appears to be very little overlap between areas of high species diversity or the presence of rare species among terrestrial and freshwater environments (Abell et al 2010), which may indicate that the mechanisms driving richness and shaping communities are not shared across classification schemes.

EFFECT OF SCALE ON ECOLOGICAL DRIVERS OF PRODUCTION

From the turn of the 21st century, there has been much more attention on the effect of the spatial scale of observation on the perceived relationships between a particular environmental variable and a particular ecological quantity (Levin 1992, Schneider 2001). With this increasing body of research is the realization that fine scale observations (e.g. at a stream reach) are often extrapolated up to larger scales at which management decisions are made (e.g. watersheds; Urban 2005, Feist et al 2010). While we often have enough information to distinguish among environmental mechanisms occurring at different hierarchical scales, it is much more difficult to

determine which of these variables are directly affecting the behaviour and life-history of aquatic organisms. Further, there are relatively few studies that attempt to untangle the effects of scale on the ecological drivers of fish production, even by simply looking for the strength of associations at different hierarchical levels. In regards to designing spatial management areas, these types of studies are critical, because they suggest at what scale management actions will be fine enough to affect fisheries, and broad enough to allow for an efficient regulatory structure. We review a few examples of these rare studies to present both the methodology used and the conclusions.

The influence of scale on Pacific salmon densities has been examined in the US Pacific Northwest for a range of salmon species and watersheds (Feist et al 2003, Firman et al 2010, Feist et al 2010). These three studies contrasted the power of environmental variables at local scales at spatial extents of 1 to 10 km^2, intermediate scales (i.e. 50 to 250 km^2) and watershed scales (i.e. 300 to 1000 km^2) to estimate the density and distribution of fish spawning redds within an entire drainage basin (i.e. 10,000 to 100,000 km^2). Importantly, as the spatial scale of observation increased, the grain of resolution did not change. The environmental variables studied included five general categories (land use, land cover, structure, climate and geology) of which each contained multiple-variables which were tested against redd counts using mixed-models including the fixed effect of habitat and the random / autoregressive component of population fluctuations over time. In all studies, suitable variables were found at each scale that could be used to estimate fish density. However, in two of the studies (Feist et al 2003, Feist et al 2010) the best models were found at the largest scale (i.e. at the watershed level). In the third study, adult Coho density was correlated strongly at all scales to the environmental variables chosen, however there was a shift in important variables at different scales, yet the general type of variable remained similar (Firman et al. 2010). For example, at local scales the density of cows near the stream reach had a strong influence on fish density, whereas at the watershed scale road density was more important. Both these variables are strongly related to land use practices, and are representations of human activity at different scales. This insight is found in a similar study by Troia and Gido (2013) which found good correlations as long as the environmental variables matched the scale of observation (i.e. broad indicators work best at broad scales). Overall, however, the fact that broader scales contributed more robust models of fishery indicators is encouraging for developing reasonable sizes of management areas, and is an insight found to varying degrees in other similar studies (Moerke and Lamberti 2006, Nakagawa et al 2014).

The importance of regional scales to predictive ecological models is also found in lake studies. Cheruvelil and colleagues (2008, 2013) studied the effect of spatial scale on the ability to predict water quality parameters in lakes in Michigan (Secchi depth, chlorophyll a, total nitrogen, total phosphorus and alkalinity; Cheruvelil et al. 2008) and across lakes and reservoirs in Maine, New Hampshire, Michigan, Wisconsin, Ohio and Iowa (total phosphorus and alkalinity; Cheruvelil et al. 2013). Note that these variables are often used to predict fisheries productivity in both lakes (e.g. Schlesinger and Regier 1982, Deines et al. 2015) and rivers (McGarvey et al. 2010). In both studies, the regional scales (i.e. ~20,000 km^2) were best at partitioning variation among classified areas, and thus were best at predicting lake water chemistry. The authors argue that regional scales are important links for extrapolating ecological drivers at local scales to continental scales, which is often required when monitoring ecosystem change. In the more recent study, the authors examined 7 classification schemes that were parameterized with local and regional environmental measurements to determine which was best at estimating the water chemistry of 2319 lakes (see Table 2). In this study, all regional parameters could also be estimated at local scales (e.g. precipitation, road density, surficial geology) and there were only three unique local scale parameters, all of which were lake specific (i.e. surface area, maximum depth, and catchment area). Like in the Pacific Northwest salmon studies, mixed effects models

were used to partition variance within-region and among-regions. Interestingly, a terrestrial (Bailey Sections), an aquatic (Hydrologic Units) and a hybrid (Ecological Drainage Units) classification scheme explained similarly large amounts of variation (~60% for phosphorus; 75% for alkalinity). Within the Ecological Drainage Units, phosphorus was best explained by a terrestrial (surficial geology), an aquatic (base-flow) and an anthropogenic (row crop agriculture) variable, while alkalinity was best explained by forest cover. These results are insightful for two main reasons. First, the best classification schemes were intermediate in size, showing that they struck a balance between high and low among region variation at small and coarse scales, respectively. This suggests that intermediate scales are best at uncovering appropriate ecological drivers of water chemistry. Second, the results demonstrate that terrestrial and aquatic variables are both needed to create robust classification schemes as well as predictive models at intermediate scales. This insight addresses the caveat from the previous section that comparing terrestrial and aquatic classification schemes ignores the fact that the mechanisms that drive each of these systems may be occurring at different scales. As such, combining terrestrial and aquatic characteristics to uncover ecological drivers of water quality or fish productivity may be the best approach.

From the same system of lakes and the same local and regional ecological mechanisms discussed in the previous paragraph, Soranno and colleagues (2010) explored how a classification scheme could be created which would delineate homogenous areas for Total Phosphorus and Chlorophyll A. The authors make an important distinction between the processes of seeking homogeneity within landscape classes for "state" versus "response" variables as well as present a system for classifying freshwater ecosystems for multi-ecosystem management and conservation. In this work, the lakes were classified by either 7 Total Phosphorus lake classes or 3 Chlorophyll A lake classes (both "state" variables), or by 3 relationships between Total Phosphorus and Chlorophyll A (a "response" variable). The predictive ecological mechanism were determined using classification and regression trees (CART) models for the two state variables, and Bayesian tree models for the response variable. Local ecological mechanisms (e.g. lake depth) were much more important to delineating state variables in comparison to the response variable in which regional mechanisms (e.g. ecoregion class and run-off) were mainly responsible for delineating homogenous areas across the landscape (Figure 5). However, even in the state variables, the Ecoregion parameter was the first selected by the CART model to differentiate among lake classes. This result highlights the importance of regional variables in driving classification schemes and predictive landscape models.

Table 2. The classification schemes at the regional scale used to test their predictive ability in estimating water quality parameters for 2319 lakes and reservoirs across the mid-west and northwestern US (Source: Cheruvilil et al. 2013).

Type	Name	Mean Area (km^2)	Number of Areas
Terrestrial	EPA Regions	163,616	4
	Omernik Level III	38,462	17
	Bailey Sections	28,365	23
	Major Land Resource Areas	22,277	29
Aquatic	Freshwater Ecoregions	109,009	6
	Hydrologic Units	13,868	47
	Ecological Drainage Units	18,544	35

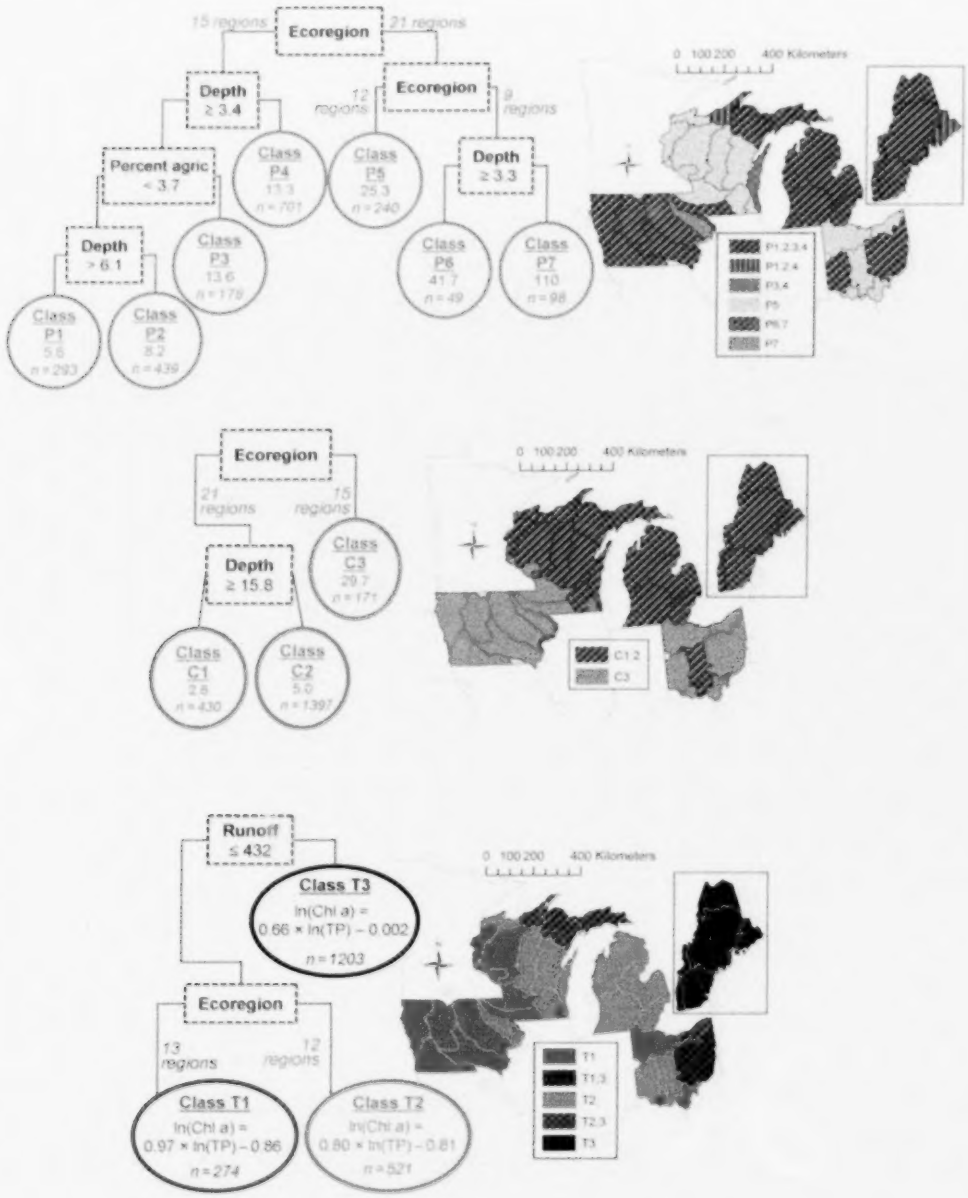


Figure 5. The classification trees (left) and maps (right) of areas within ecoregions that correspond to Total Phosphorus (top row) and Chlorophyll A (middle row) state variables, and a Total Phosphorus and Chlorophyll A response variable. (Source: Soranno et al. 2010, note that the Figure has been modified).

ECOLOGICAL DRIVERS OF PRODUCTIVITY FROM SOLICITED CONTRIBUTIONS

The management of fish productivity across any landscape size that includes multiple populations and communities, will likely require an understanding of the ecological mechanisms that influence productivity, rather than the application of stock-specific approaches that estimate the productivity of each population through statistical models. In Canada, landscape models of highly valued freshwater recreational species exist and have been developed mostly to manage fisheries at the provincial scale (e.g. Lake Trout, Shuter et al. 1998; Walleye, Lester et al. 2014; Smallmouth Bass, Chu et al 2006; all Ontario fish communities, de Kerckhove et al. 2015). In this section of the report, insight is provided on a particular driver of productivity, and how spatial units of management may relate to them.

First, Mark Hoyer presents how primary productivity can be estimated at the scale of the Ecoregion, and drives observed levels of fish biomass in Florida, USA. He demonstrates that the trophic status of lakes remains an important predictor of fish biomass and fisheries production in Canada and the United States. He concludes that chlorophyll, morpho-edaphic and secchi depth based models can be used at broad spatial scales to classify lake systems. However, Hoyer points out that in some cases (e.g. chlorophyll), the trophic driver alone may only explain a low level of variation in fish biomass (i.e. ~17% in total fish biomass), and as such, other landscape features should be used within the classification system or predictive model.

Next, Kyle Wilson presents how elevation and latitude influence lake fish productivity in British Columbia, and suggests that socio-economic considerations may also fall within management regions (e.g. fish life-history characteristics are going to be influenced by multiple sources of ecological and anthropogenic mechanisms). Wilson discusses how climate and elevation are strong drivers of fisheries productivity in the northern limits of fish species' ranges because a change in temperature can greatly affect existing constraints on growth (e.g. the length of a growing season). However, in southern regions, where existing constraints may be fewer (e.g. year-long growth seasons), changes in climate or elevation may be less important drivers of fish life-history. This relationship is further confounded by socio-economic mechanisms such as angler effort. In southern British Columbia, the Rainbow Trout populations have the best environmental conditions for growth, however they are also highly exploited by a recreational fishery. As such, the northern populations exhibit the largest fish. Wilson concludes that management regions will need to be designed taking three main considerations: 1) the life history variation of the relevant fish species, 2) the population's location upon the landscape (i.e., latitude, topography, elevation), and 3) the relative influence of climate or fishing effort (as a confounding factor) on regulating the productivity of the population of interest. He notes that British Columbia currently has 8 Management Regions that blend a spatial resolution between 5 physiographic zones and the 14 Biogeoclimatic zones.

Next, Dak de Kerckhove combines the previous two contributions by presenting how nutrients and climate are addressed under the Metabolic Theory of Ecology (MTE), and thus may provide a promising framework for estimating fish productivity across landscapes. The use of the Area-Per-Individual and Morpho-Edaphic models is presented in the context of the MTE. de Kerckhove suggests that with the knowledge of the quality of the habitat, the typical range of fish sizes within a community, and the thermal habitat of the members of the community, the maximum standing stocks of local fisheries can be estimated. However, he points out that it is worthwhile to study the implications of the Van't Hoff Arrhenius equation with the MTE in the context of climate change and habitat quality. If habitat quality is maximized, fisheries productivity should be higher in warmer climates, but fish density should be lower. de Kerckhove demonstrates with data from the Athabasca River that although overall fish densities are lower

than in rivers across Canada, the slopes of the relationship between fish size and density are flatter, indicating that there are relatively higher densities of larger fish in this northern climate (although note that in this case, habitat quality is not equivalent across the datasets, which suggests a strong hypothesis for the overall lower density).

Next, Cindy Chu joins de Kerckhove in presenting how the observed catch from gill net surveys across Ontario watersheds, once scaled up to the level of Ontario's Fisheries Management Zones, matches the expectations of fisheries productivity from climatic-morpho-edaphic models as long as fish mortality from the recreational harvest is also accounted for. This contribution re-enforces the insights brought up by Mark Hoyer and Kyle Wilson, and demonstrates that fisheries production models (e.g., the morpho-edaphic index) combined with knowledge of socio-economic mechanisms (e.g., a recreational fishery) can be used to make reasonable predictions of the status of fisheries among management units. In this particular case, the management unit at the size of an ecoregion seems appropriate.

Finally, Ken Minns proposes a framework for applying estimates of productivity within the FPP policy with a call for more research on understanding drivers of Production to Biomass (P:B) ratios. Minns points out that it is a much less difficult task to use common fish survey methods to make site-specific biomass estimates and then use theoretical P:B ratios to calculate site-specific rates of production.

NUTRIENT DRIVERS OF LAKE PRIMARY PRODUCTIVITY AND FISH BIOMASS

Contributed by Mark Hoyer, Director of the Florida LAKEWATCH program, University of Florida

Pioneers in limnology recognized that regional conditions influence lake trophic status (Naumann 1929). Geology, soil characteristics, vegetation and climate are some of the major factors determining the basic nutrient concentrations, chlorophyll concentrations and thus productivity of lake systems (Moyle 1956; Omernik 1987; Canfield and Hoyer 1988). The US EPA began to develop ecoregions because there was a need to provide a geographic framework that would allow state and regional water resource managers to structure their regulatory programs more effectively by accounting for the regional differences in potentials and capacities of the environment (Omernik 2004). The development of this framework was based on the following logic:

- The quality and quantity of water at any point reflects the aggregate of the characteristics up-gradient from that point.
- Water quality and quantity will tend to be similar within areas where this aggregate is similar.
- Therefore, for effective water resource research, assessment, and management, these regions within which there are similar geographical phenomena that affect water quality and quantity must be defined.
- Reference watersheds and areas within each can then be identified to determine expectations, criteria, and appropriate management practices (Hughes et al 1986, Hughes 1995, Omernik 1995, Bryce et al 1999).

Similarly, a National Ecological Framework was developed for Canada (Marshall et al. 1999) including the following:

- Ecozone (15 units); At the top of the hierarchy, it defines the ecological mosaic of Canada on a sub-continental scale. They represent an area of the earth's surface representative of large and very generalized ecological units characterized by interactive and adjusting abiotic and biotic factors. Canada is divided into 15 terrestrial ecozones.

- Ecoprovince (53 units); A subdivision of an ecozone characterized by major assemblages of structural or surface forms, faunal realms, and vegetation, hydrology, soil, and macro climate. For example, the Newfoundland ecoprovince (no. 6.4) is one of six ecoprovinces within the Boreal Shield Ecozone.
- Ecoregion (194 units); A subdivision of an ecoprovince characterized by distinctive regional ecological factors, including climate, physiography, vegetation, soil, water, and fauna. For example, the Maritime Barrens ecoregion (no. 114) is one of nine ecoregions within the Newfoundland ecoprovince.
- Ecodistrict (1021 units); A subdivision of an ecoregion characterized by a distinctive assemblages of relief, landforms, geology, soil, vegetation, water bodies and fauna. For example, the Jeddore Lake ecodistrict (no. 473) is one of five within the Maritime Barrens ecoregion.

Developing a National Ecological Framework for Canada (NEFC) is described as: "a process of delineating and classifying ecologically distinctive areas of the Earth's surface. Each area can be viewed as a discrete system, which has resulted from the mesh and interplay of the geologic, landform, soil, vegetative, climatic, wildlife, water, and human factors, which may be present. The dominance of any one or a number of these factors varies with the given ecological land unit. The holistic approach to land classification can be applied incrementally on a scale-related basis from site-specific ecosystems to very broad ecosystems" (Wiken 1986). There were 26 attributes included in the database used to develop the NEFC, covering five general categories, including: area of each ecological unit (2); climate (14); physical landscape characteristics (8): land cover (1); and population (1).

In Florida, Griffith et al. (1997) identified 47 lake regions each with lakes having unique nutrient characteristics and recently Bachmann et al. (2012) consolidated these regions into six total phosphorus and five total nitrogen zones that the Florida Department of Environmental Protection is now using with the new US EPA's numeric nutrient criteria to determine natural background nutrient concentrations in Florida lakes. This regional approach to classifying the trophic status of lakes has been successfully used in many locations around the world (e.g., Minnesota; Heiskary and Wilson 2008, Nebraska; Bulley et al. 2008, Europe; Nogas 2009, China; Huo et al. 2013 and others).

Conventional wisdom suggests that the base fertility of a lake (trophic status) is a primary driver for the abundance of aquatic organisms including but not limited to: zooplankton abundance (Canfield and Watkins 1984), fish populations (Bachmann et al 1996), bird abundance (Hoyer and Canfield 1994) and even populations of top predators like the alligator (Evert 1999). All of these results support the predictions of Fretwell (1987), who suggested that as nutrient levels increase among systems, the abundance of organisms including top predators would also increase.

Many different models have been developed to predict abundance of biological organisms, primarily fish in lake systems, based on water chemistry parameters in relation to some morphometric variables. Rawson (1952) originally used total dissolved solids as a predictor variable and others used specific conductance, nutrient concentrations and chlorophyll concentrations or algal biomass (e.g. Jones and Hoyer 1982). Of these, the morpho-edaphic index (MEI: total dissolved solids or conductivity divided by mean depth) has been most often used to predict fish biomass in Canadian lakes (Ryder et al 1974), large temperate reservoirs (Jenkins 1967), and African lakes (Ryder et al. 1974). The underlying assumption for the use of the MEI is that it has the ability to estimate the base primary production of an aquatic system. If any limnological factor (anthropogenic or natural) impacts the amount of limiting nutrient in relation to total dissolved solids/conductivity then the model is not as useful (Jones and Hoyer

1982, Lara et al. 2009). Thus a better approach would be to use actual limiting nutrient concentration (phosphorus and/or nitrogen) or actual measures of algal abundance (chlorophyll concentrations) as predictors of fish biomass.

Recently, Hoyer et al. (2011) used chlorophyll concentrations to predict fish abundance in Florida lakes. Hoyer et al. (2011) added the suggestion that for broad scale analyses ecoregions and/or nutrient zones could be used as a rough estimate of fish abundance in lakes. For example, lakes located in nutrient poor regions tended to have less fish than those in nutrient rich regions. Grasshopper Lake resides in Lake Region 75-09 (Ocala Scrub, lakes ranging in total chlorophyll concentrations from 4-7 µg/L) had a lower average total fish electrofishing catch per unit effort (CPUE) of 19.2 kg/hr than Lake Weohyakapka's total fish CPUE of 84.5 kg/hr, which resides in Lake Region 75-35 (Kissimmee/Okeechobee Lowland, lakes averaging total chlorophyll concentrations >30 µg/L). Thus, using the ranges in chlorophyll concentrations for the lake region in which a lake resides and the best trophic state parameter variable versus fish biomass model will give lake managers a general idea of the level of fish biomass that can be expected in individual lakes. However, there is a tremendous amount of variance in these relations with chlorophyll, Hoyer et al. (2011) showing chlorophyll accounting for only 17% and 9% of the variance in total fish CPUE and sport fish CPUE, respectively. Other abiotic and biotic factors impacting fish abundance need to be added to this first assessment of base productivity to better estimate potential fish abundance, especially over large spatial scales. Included in these factors but not limited to them are: altitude, latitude, growing degree days, ice cover in relation to lake depth, annual precipitation, habitat availability for spawning and recruitment and others (Marshall 1996, Almodovar et al. 2006, Gaeta et al. 2014, Wurtsbaugh et al. 2015).

The primary key to using an Ecoregion approach to estimate lake trophic status and then potentially fish biomass in lakes is in the ability to obtain enough data within each Ecoregion to determine if the trophic state of lakes within each Ecoregion shows significant differences (Bachman et al. 2012). One potential approach is with the use of water clarity measurements estimated with a Secchi disk as these measurements are directly related to trophic status in the absence of high levels of color or suspended solids (Canfield and Bachmann 1981 Hoyer and Jones 1983) and are relatively easy to obtain. Recently, Bigham et al. (2015) compiled extensive (>1,000,000 readings) Secchi data from, local, state and national lake assessment programs and many volunteer water quality monitoring programs across the United States. These data were used to examine regional patterns across the nation and they showed some significant differences among US EPA's level III ecoregions. Similarly long-term citizen collected Secchi data revealed geographic patterns in in the Upper Midwest, USA (Lottig et al. 2014). Another potential advantage with using Secchi depth measurements to estimate lake trophic status is the ability to estimate Secchi depth values with remote sensing technologies, which can easily cover large inaccessible areas on a regular basis (Knight and Voth 2012, McCullough et al. 2013).

The secondary key to using an Ecoregion approach to estimate lake trophic status and then potentially fish biomass in lakes is to develop model/models with the ability to estimate fish biomass from trophic state variables (Jones and Hoyer 1982, Hoyer et al. 2011). This will require collecting or mining comparable fish biomass estimates in lakes with available trophic state data. These models also have to take into account other variables important to fish production in lakes. Much of these data already exist and with a well developed National Ecological Framework for Canada, a pilot study pulling them all together would yield a good first approach at estimating fish biomass across the large spatial areas of Canada.

INFLUENCE OF LATITUDE AND ELEVATION ON LAKE FISH PRODUCTIVITY

Contributed by Kyle Wilson, Ph.D. Candidate, University of Calgary

Fish populations adapt to local environments leading to optimal growth and survival schedules that might vary in any given environment (Roff 1983). Life history theory shows that individual growth rates are dynamically linked to population-level rates, such as total annual survival and sustainable harvest rates (Shuter et al. 1998; Post et al. 1999; Lorenzen and Enberg 2002; Walters and Martell 2004; Lester et al. 2014). This linkage is generally explained by relationships between individual body-size and predation risks, survival (Lorenzen 1996), competitive interactions (Post et al. 1999), and fecundity (i.e., both abundance and size/quality of reproductive effort; Lester et al. 2014). As temperature plays one of the most fundament roles in regulating the growth and survival of freshwater fish (Clarke and Johnston; Lorenzen In Press), variation in climate among and within landscapes (e.g., states or provinces) can influence the productivity of freshwater fish populations (Shuter et al. 1998; Randall and Minns 2000; Lester et al. 2014).

Patterns in climate (e.g., local annual temperature trends) are influenced by topography and the position of a waterbody upon its broader landscape (MacArthur 1972). Two of the most common landscape-level characteristics associated with climatic variation are latitude and elevation. For example, latitude and elevation influence the amount of thermal energy that reaches a given geographic area (MacArthur 1972) thereby influencing local surface water temperatures, as air and water temperatures are correlated (Shuter et al. 1983). Hence, variation in landscape-level features, such as latitude and topography, can mediate the duration of the growing season, the thermal energy that reaches an aquatic ecosystem, and fish metabolism and physiology (Conover and Present 1990; Clarke and Johnston 1999). Waterbodies at lower latitudes and/or lower elevations generally experience warmer climates and longer growing seasons than waterbodies at higher latitudes and/or higher elevations. Local watershed factors, such as hydrologic connectivity (e.g., a northern lake connected by a more southerly warm river) and coastal currents (e.g., a northern coastal fishery subject to warm-water current) can counter landscape-level gradients, but general patterns still emerge across latitudinal and elevation clines. As the life-history of many freshwater fishes is highly plastic (e.g., growth rates differ between favorable and poor environments), variation in either of these landscape-level characteristics is associated with variation in the productive capacity of inland fishes. All else equal, fish in warmer waters tend to grow faster, survive better, and mature earlier, and are thereby more resilient to harvest than fish in colder waters. Hence, variation and changes in climate can have a strong effect on individual growth and survival, and on the fish abundances and biomass available for harvest (Walters and Post 1993; Lorenzen 1996; Shuter et al. 1998; Post et al. 1999; Lester et al. 2014).

British Columbia appears to have some of the highest topographic and climatic variation in Canada. Due to complex topography that structures high variation in climate over short distances, British Columbia is a particularly useful case study to evaluate landscape-level variation in latitude and elevation and effects to fish productivity. For example, there are five recognized physiographic zones including the northern plateaus and mountains, the northern Great Plains, the southern interior plateau, the southern Columbia Mountains and Rocky Mountains, and the Coast Mountains and islands (Pike et al. 2010). In addition, British Columbia has 14 recognized Biogeoclimatic zones that partition the physiographic zones further based on hydrology, biodiversity, climatic trends, and ecosystem function (Pike et al. 2010). The large contrast in topography, latitude, and elevation drives substantial climatic gradients including a mean annual air temperature that ranges from -9°C in the north to +9°C in the lower mainland (Pike et al. 2010). Since thermal energy, ecosystem productivity, and fish growth are highly correlated, growing degree-days above a baseline temperature (often 5°C in fish ecology) is a

useful metric for describing a waterbody's thermal energy and productivity that helps account for a waterbody's latitude and elevation. For example, there is a substantial gradient in the duration (i.e., number of days) and magnitude (i.e., temperature levels) of the growing season across the 14 Biogeoclimatic zones in British Columbia, and this gradient is captured by a six-fold difference in growing degree-days > 5°C (from 301 DD >5°C in Interior Mountain Alpine to 1,965 DD >5°C in Coastal Douglas Fir).

The provincial management of British Columbia's fisheries is divided into 8 independently-administered Management Regions that blend a spatial resolution between the 5 physiographic zones and the 14 Biogeoclimatic zones (Parkinson et al. 2004). Many popular fishing destinations in British Columbia are located in the southern interior plateau (Regions 1, 3, 4, 5, and 8), a region of the province that is particularly warm with many lakes and rivers located at low elevation. As well, British Columbia has popular cold-water fisheries located in the northern and central plateaus and mountains (Regions 5, 6, 7A, and 7B), in addition to high alpine lakes throughout the Coast, Columbia, and Rocky Mountains.

Both Rainbow Trout and Lake Trout (Char) are commonly sought after game fish that provide important recreational fisheries to British Columbia. The provincial range of both species spans hundreds of lakes with latitudinal overlap around Region 5. Generally, Lake Trout persist in lakes among the northern physiographic zones, while Rainbow Trout persist in lakes and rivers towards the south, but both species can inhabit low-elevation lakes (i.e., valley) and high-elevation lakes (i.e., alpine). Recent work on both species reveals how climatic gradients associated with latitude and topography regulates plasticity in demographic rates such as fish growth, survival, and, ultimately, the quality of the fishery. We review such work to guide the development of optimal spatial units to manage for fisheries productivity in relation to latitudinal, elevation, and topographic clines.

As previously mentioned, landscape-level variation in climate can drive plasticity in individual growth rates. Hence, individual growth can provide a surrogate indicator for fishery productivity, or be used directly to help calculate production rates per unit area (Minns et al. 2011). Using growing degree-days as a climatic metric and biphasic growth, Ward (2014) found a nearly three-fold improvement in juvenile growth rates for British Columbia Rainbow Trout in warm water lakes at low elevation compared to colder water lakes at high elevation. Interestingly, this high variation in growth rates was found across only a two-fold gradient in growing degree-days (from 1,036 to 1,964 DD >5°C), indicating that the six-fold gradient that persists across the entire province might further influence growth variation. Assuming biphasic growth, juvenile growth rates in British Columbia Lake Trout appear subject to similar variation as growth rates increase from 20 $mm \cdot yr^{-1}$ at 400 DD >5°C to 40 $mm \cdot yr^{-1}$ in lakes with 1,000 DD >5°C (Kyle Wilson, unpublished data). Furthermore, both Rainbow Trout and Lake Trout mature at younger ages in waterbodies with a longer growing season with Lake Trout age-at-maturity in lakes at 800 m elevation ~12 years, whereas populations at ~1,600 m elevation mature ~18 years of age. (Ward 2014; Kyle Wilson, unpublished data).

Landscape-level climatic patterns cause variable environments and plastic expression of fish life history that can influence fish productivity. This phenomenon is not exclusive to British Columbia nor to salmonids, and should be an important consideration for developing spatial units for managing fisheries productivity for a variety of fishes and life history strategies. North American Walleye populations grow faster and mature at younger ages in warm-water inland landscapes located in the Midwest United States, than Walleye populations located in northern Ontario and Quebec (Lester et al. 2014). Interestingly, variation in these two landscape-level features appears to lead to changes in risk-sensitive foraging behaviour leading to risk-taking behaviour when the growing season is short (e.g., at high latitudes), and risk-averse behaviour for longer growing seasons at lower latitudes (Conover and Present 1990; Mogensen et al. 2013). Such

behavioural differences clearly influences fish catchability, meaning fish at northern latitudes or higher elevations can be more easily overfished partly due to changes in foraging behaviours (Mogensen et al. 2013).

The comparative latitude of a fish population to the extent of the species' native latitudinal range can modify how climate might regulate the demography of that population (MacArthur 1972). Generally, temperature mediates growth and survival in fish populations distributed poleward to their native geographic range. For example, Brown Trout at the polar extent of their range displace Arctic Char occurring near their southern range due to the Arctic Char's lower tolerance for warming winter temperatures in Norwegian lakes (Urban et al. 2011). Similarly, Welch et al. (1998) found the southern range limit for sockeye salmon in the Pacific Northwest has shifted northward due to the salmon's low tolerance of warming temperatures creating a metabolic stressor on energy allocation. Demographic rates in equatorward populations (i.e., populations located at the equatorial extent of their range) might not be strongly influenced by temperature due to increased amounts and increased stability in the thermal energy that reaches the system (Venturelli et al. 2010). Individual condition, an indicator for productivity (Minns et al. 2011), of Largemouth Bass in Florida (the equatorward extent of their native range in North America) was not driven by temperature because most Florida lakes have high and stable temperatures and subsequently long growing seasons (Boucek et al. In Review). Hence, identifying Biogeoclimatic zones that describe similar climate patterns for common regions can describe similarities in demographic rates and productivity of many northern fishes, but this will depend on the environmental characteristics of a population's location relative to a native geographic range.

Latitude, topography, and elevation also influence social-ecological factors related to fishery harvest, as human population centers are non-randomly distributed across landscapes. This reveals a key linkage between social factors, harvest pressure, and fish populations that affects metrics of fishery productivity such as body size, condition, and relative abundance (CPUE; Beardmore et al. 2013). For example, recreational anglers in northern BC are more harvest-oriented and spend more days fishing, but total fishing effort is higher in southern BC due to high human populations closer to Vancouver (Post et al. 2008; Ward et al. 2013). Furthermore, high mountain alpine lakes tend to receive less effort than similar lakes that are lower in valleys, likely due to access restrictions (Beardmore et al. 2013; Dabrowska et al. 2014; Mee et al. In Press). Given that long-term data to compare impacted (fished) systems to natural (unfished) systems is limited (Minns 1997; Minns et al. 2011), social factors can confound productivity assessments that rely on snapshot comparisons between low-effort (i.e., close to pristine) and high-effort (i.e., impacted) regions or lakes.

The joint effect of variation in climate and variation in social factors can be contrasted using fishing quality models (Parkinson et al. 2004; Askey et al. 2013; Wilson et al. 2016). Fishing quality is a metric that directly combines the trade-off between fish body size and fish abundance (CPUE), two traits that correlate to fish productivity. This trade-off emerges from density-dependent growth and survival in response to a combination of harvest mortality and favorable climate and environments (Wilson et al. 2016). The old fishing adage 'you can catch a big fish or you can catch a lot of fish, but you can't catch a lot of big fish' explains the usefulness of this type of metric. Specifically, there is an emergent equal-quality curve expressing the trade-offs between fish size and fish abundance within a common region of water bodies. Moving along this curve denotes changes to the population mediated by density-dependent growth and survival, but as long as the population falls at or near this curve then quality has not changed (i.e., trophy-fish harvest reduces fish size but this could be offset by compensatory improvements in fish abundance). Impacts to the system may alter fish size, or it may alter fish abundance, but this may or may not have impacts to the quality of the fishery for users of the resource. Using fishing quality metrics, Wilson et al. (2016) found that two equal-quality curves

co-occur in the British Columbia Rainbow Trout fishery, one curve in two southern management regions and the second curve in two northern management regions. Interestingly, though climate may be more favorable to fish growth in the southern landscapes, the fish populations in the northern landscapes were more abundant and reached larger sizes. This counter-gradient pattern is directly associated with angling pressure being concentrated in southern British Columbia, depleting lakes of more fish and larger fish. Such a pattern reveals that social factors, like angling effort, can have a strong confounding influence on approximating metrics of fish productivity, e.g., CPUE and body size, and that angling effort can be associated with latitudinal gradients. For the purposes of British Columbia Rainbow Trout, these dynamics overlap the independent management regions and suggest that optimal spatial resolution to account for these dynamics occur larger than independent management regions but smaller than the entire province.

Changes in topography and latitude can influence climate, fish populations, and social-ecological factors, like fisher behaviour. Hence, selecting optimal spatial units for managing the productive capacity of any fishery should consider how climate and human behaviour mediate changes in productivity metrics, like CPUE or growth rates. Specific to British Columbia, Management Regions 3 and 8 share similar characteristics (including effort dynamics) and might be considered an operational spatial unit (i.e., a unique fishing landscape), and Management Regions 5 and 7 might be a unique fishing landscape, but the dynamics regulating these two 'landscapes' appeared to operate different from one another. Further considerations for differences in individual growth rates, harvest pressures, and climate variation may reveal that a finer-scale resolution is needed to account for differences in productive capacity. However, we can currently conclude that the spatial resolution of the current 8 independent management regions may not parsimoniously explain key attributes of British Columbia's Rainbow Trout fishery. Generally, we suggest that Biogeoclimatic zones or physiographic could provide a starting point for delineating plausible differences in fish productivity alongside the distribution and magnitude of fishing effort, or total harvest pressure, within those zones. Assessing fish productivity models within an Information Theoretic approach could help find the most parsimonious spatial unit that explains the productivity metric (i.e., fishing quality, or individual growth rates). Because not all fishes or populations of interest are affected by the same landscape-level drivers, such delineation will need to be contextualized to 1) the life history variation of the fish species, 2) the population's location upon the landscape (i.e., latitude, topography, elevation), and 3) the relative influence of climate or fishing effort (as a confounding factor) on regulating the productivity of the population of interest.

USING THE METABOLIC THEORY OF ECOLOGY TO DEFINE SPATIAL UNITS

Contributed by Dak de Kerckhove, Research Scientist at the Ontario Ministry of Natural Resources and Forestry

The observation that larger organisms tend to occur at lower densities is generally found across all taxonomic groups. As such, the mechanisms that lead to these patterns have been widely discussed over almost a century of ecological progress with applications to forestry (e.g. the self-thinning hypothesis) and fisheries (e.g. size-spectrum ecological indicators). More recently, this observation was explained under the concept of a Metabolic Theory of Ecology (Brown et al. 2004) in which the metabolism of organisms is thought to be the mechanism that unites two fundamental ecological currencies: the flow of energy through ecosystems and the availability of resources. Using well understood biological scaling laws (i.e. allometric and energetic relationships) the metabolism of individuals has a direct influence on a variety of ecological properties including population growth rates and community dynamics. This theory helps explain some of the few unequivocal laws of ecology including exponential population growth (Turchin

2001) and species-area relationships (Hutchinson and MacArthur 1959). The strength of this theory is that within its framework one can estimate a wide range of ecological parameters using mainly the average body size of the members of a particular community (*M*), temperature (*T*) and the availability of resources (*R*). From its introductory paper, carrying capacity (*K*) is described as:

$$\begin{pmatrix} Carrying \\ Capacity \end{pmatrix} = \begin{pmatrix} Normalization \\ Coefficience \end{pmatrix} \begin{pmatrix} Limiting \\ Resources \end{pmatrix} \begin{pmatrix} Scaled \\ Body\ Mass \end{pmatrix} \begin{pmatrix} Van't\ Hoff - \\ Arrhenius\ Relation \end{pmatrix}$$

or in proper notation:

$$K = (i_0)(R)\left(M^{-\frac{3}{4}}\right)\left(e^{\frac{E}{kT}}\right)$$

where *E* is the activation energy from aerobic respiration and *k* is Boltzmann's constant. From this equation, with the knowledge of the quality of the habitat, the typical range of sizes within a fish community (i.e. the size spectrum), and the thermal habitat of member of the community, the maximum standing stocks of local fisheries can be estimated. In some cases, the productivity of these stocks can be estimated directly using Production:Biomass ratios, which scale allometrically with metabolism as long as the influence of temperature is also controlled:

$$\frac{P}{W} = (i_0)\left(M^{-\frac{1}{4}}\right)\left(e^{\frac{-E}{kT}}\right)$$

where *P* is production and *W* is standing stock biomass. These equations suggest that carrying capacity and production will change with average body size and climate, although note from the exponent on the Van't Hoff Arrhenius Relation that they will change in different directions with temperature (i.e. in hotter climates productivity increases but density decreases, all else being equal).

The climate and resources side of this equation has been observed in other classic relationships in fisheries, including the climatic-morpho-edaphic index from Schlesinger and Regier (1982). In their work, sustainable yields of fisheries changed predictably with climate, lake depth and the total dissolved solids concentration of the water, which formed zones of productivity across North America, increasing from the north to the south (see Figure 6). In terms of defining spatial units of management, this approach would work best within broad physioclimatic areas or ecozones in which boundaries were defined by change in geology and climate. While this necessary higher level of resolution typically led to much criticism of the morpho-edaphic index, it would support its use in this context and direct which type of productivity estimates could be appropriate, and which others wouldn't. For example, this approach was used to estimate the total productivity of all the lakes within Ontario Fisheries Management Zones, which are each roughly the size of an ecoregion (de Kerckhove et al. 2015). Another potential weakness of Schlesinger and Regier's (1982) equation is that for some communities, the effect of climate may be buffered by thermal refuges within local habitats (e.g. cold springs, seepages and hypoliminions, cooler habitats at higher elevations) yet there is no flexibility in the relationship to account for this.

It is worth noting that the body-size component of the Metabolic Theory of Ecology may be implicitly addressed within research on the morpho-edaphic index. Much of the verification and application of this model occurs on Lake Trout data within Ontario, for which a strong relationship between maximum body-size and lake size is well known (Shuter et al 1998). As area based estimate of productivity from the morpho-edaphic index decline with lake depth this

would match the negative one-quarter exponent on the P/W equation presented above. However, generally the body-size side of the Metabolic Theory of Ecology equation has been explored much less as a means to calculate productivity, even though it's commonly used as an indicator of productivity (Fulton et al. 2005, de Kerckhove 2015).

One important reason that the equations from the Metabolic Theory of Ecology are rarely used to derive explicit estimates of productivity is that even in the 2004 introductory paper the authors state that general allometric relationships should not be used in applied contexts. From their perspective, there is too much variation in actual estimates of standing stock biomass across a landscape likely due to uncertainty in how to estimate the normalization coefficient (i_0) or properly characterize the limiting resource (R). However, despite this caveat, principles from the Metabolic Theory of Ecology have been applied with success to ocean fisheries over the last decade, and more recently in freshwater ecosystems. For example, changes in the size-spectrum of fish communities is a robust ecological indicator (Fulton et al 2005) and has been linked to overfishing (Bianchi 2000), environmental degradation (Ellis, L. et al. unpublished manuscript[1]) and predator-prey interactions (Giacomini et al 2015). Further, progress in understanding how to separate relatively independent communities from one another within a local area (e.g. benthic vs pelagic food webs), has led to improvements in verifying the framework's predictions (Brown and Gillooly 2003, Blanchard et al. 2009). Last, there are multiple ways to estimate community production, so it should be possible to apply the theory while concurrently testing some of the assumptions with alternate methods. For example, the authors of the initial framework note that a classical approach using Leslie matrices to estimate population productivity should give similar production estimates to the allometrically and temperature-controlled scaling of production:biomass ratios. Leslie matrices or simple life-history simulations parameterized with allometrically scaled standing stocks have been successfully applied by Fisheries and Oceans Canada (Velez-Espino and Koops 2009), and by industrial scientists (Total E&P Canada, 2014). If so, using the allometric and thermally-controlled relationships should allow for estimates of productivity regions around Canada similar to those from Schlesinger and Regier (1982), but with more freedom to define the normalization coefficient (i_0) and the limiting resources (R), and include the effects of elevation changes or thermal refuges on the Van't Hoff – Arrhenius Relation ($e^{E/kT}$).

The approach used by government and industrial scientists in Canadian freshwater fisheries research is the Area-Per-Individual models (*API*) which focusses on the observed relationship between body-size and density, yet also attempts to estimate the limiting resources function (R) within the Metabolic Theory of Ecology framework. The approach was developed by Fisheries and Oceans Canada scientists to evaluate the viability of aquatic habitat for species at risk (Minns 2003). The API approach is typically linked to habitat quantity and quality in the following manner:

1. Allometric relationships between the average body-size of the fish within a community (in grams) and their density (in numbers per hectare) in undisturbed habitats are derived using global datasets (see Figure 2 in Randall et al. 1995; Figure 7 in this document). If density is inverted (from #/ha to ha/#), these relationships represent the average pristine area required to sustain an average fish within the community. Therefore the API is reported as an area per fish (i.e. m^2).

[1] Ellis, L., C. Chu and D.T. de Kerckhove (2017). The effectiveness of terrestrial protected areas for lake fish community conservation. Conservation Biology. Unpublished manuscript (under review).

2. If the habitat quality and quantity within a particular area is known, various approaches (Habitat Suitability Models, Logistic Regressions of Habitat Occupancy) can be used to calculate the existing habitat in relation to a pristine habitat metric (e.g. Weighted Usable Area). For example, if a Habitat Suitability Index (HSI) rates a habitat between 0 for unsuitable and 1 for ideally suited, one can assume that the allometric relationship was generated for an HSI value of 1. Given that HSI relationships are often based on observed or predicted site occupancy, as the habitat index decreases, the amount of sub-ideal habitat needed to support an average fish from the community should increase. To continue the example, if the HSI is assessed at 0.5, than it will take twice the API to sustain an individual from the community. This approach is called a "habitat-linked API model".

Figure 6. Isolines showing the upper limits to maximum sustainable fish yield (kg/ha/yr). Note coastal effects. Source: Schlesinger and Regier 1982.

The approach outlined above assumes that relationships between habitat quality and critical resources per individual are generally linear. For some resources, this relationship is intuitively reasonable. For example, if an herbivore fed on sessile patches of a particular plant they would require larger foraging areas as the density of patches decreased. For others, there may be confounding effects, particularly at the extremes of the relationship, which cause significant deviations from linearity. For example, the suitability of spawning habitat can be confounded by over-crowding of spawners. However, properly designed HSI models should be able to address much of the non-linearity because individual suitability indices are typically not linear. This allows the HSI to fit well with the *R* component of the carrying capacity equation presented above.

At their core, habitat-linked API models are based on typically small spatial scales that focus on local communities, but this has more to do with the confines of the habitat model than the API relationship. In closed systems, API models may focus on only a portion of a lake (i.e. pelagic,

benthos or littoral) depending on how well these habitats are coupled to each other. Rarely, however, would the API model extend to a series of lakes. In open systems, API models may also only focus on particular type of habitat, especially if the fish community is expected to change under environmental gradients (e.g., longitudinal changes in riverine systems). However, in all these systems the same basic allometric relationship might be used. Scaling up to the carrying capacity model, it would be important to limit the spatial range and community composition of each analysis only so far as to ensure that the organisms selected as the community all fed on a common source of energy. This is particular important if an ideal relationship (i.e., $M^{-3/4}$) will be used. Alternative to using ideal relationships, the observed the changes in density per body-size for the communities in question could be used. The observed exponents should thus hold the influence of multiple trophic levels being included in one analysis (i.e., include the inefficient transfer of energy from autotroph up through food webs, as shown in Brown and Gillooly 2003). Randall and colleagues (1995) derived the basic API relationships for lakes and rivers using studies from across the globe. These relationships formed the foundations of other models for which more localized habitat and fish community data were used to derive a more site-specific density, standing-stock biomass and fisheries production estimates (Minns 2003, Velez-Espino and Koops 2009, Total E&P Canada 2014, van der Lee and Koops 2015).

While the 1995 API relationships has proven itself to be of great value, it is unlikely that one ideal relationship between body size and density holds across climatic and geomorphic gradients (given the insight from the Metabolic Theory of Ecology and our discussion of the morpho-edaphic index). A recent model in the lower Athabasca River watershed (Alberta, Canada) required a calibration of the API relationship because stream fish densities were often much lower than those found in other parts of the world (Total E&P Canada 2014). The lower Athasbasca River is located at a northern latitude and flows through muskeg habitats which are known to be of a relatively lower productivity. Using data from tributaries of the Lower Athabasca River, and from the original dataset from Randall et al. (1995), gradients in fish density among regions can be easily observed (Figure 7). The slopes of the relationship in this observation become shallower at colder temperatures, which suggest that habitat capacity is relatively higher for large organisms relative to smaller ones in colder environments. This conclusion is consistent with the Metabolic Theory of Ecology, and is admittedly unintuitive (Brown et al. 2004). The Van't Hoff – Arrhenius Relation is positive in our density equation (K) suggesting relatively higher carrying capacities at colder temperatures. The justification of this effect is that at colder temperatures the metabolism of the organisms is slower and therefore fish tissue isn't turned over as fast, and higher densities of larger organisms can thus be supported. However, it is important to remember that the effects of habitat and resource availability are not yet included. In our observation from the lower Athabasca River tributaries, the normalization coefficient (i_0) and limiting resources (R) clearly reflects the lower availability of resources to the fish and thus decreases the height of the curve. With more studies of this kind, the nutrients that drive these two coefficients could perhaps be identified, and thus assist with setting ecological zones of productivity following the Metabolic Theory of Ecology framework.

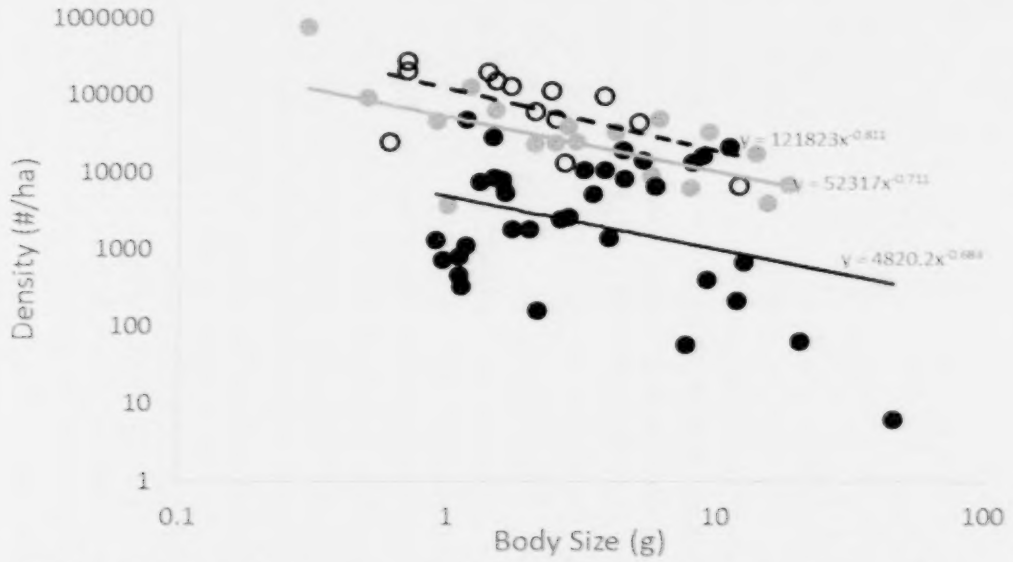
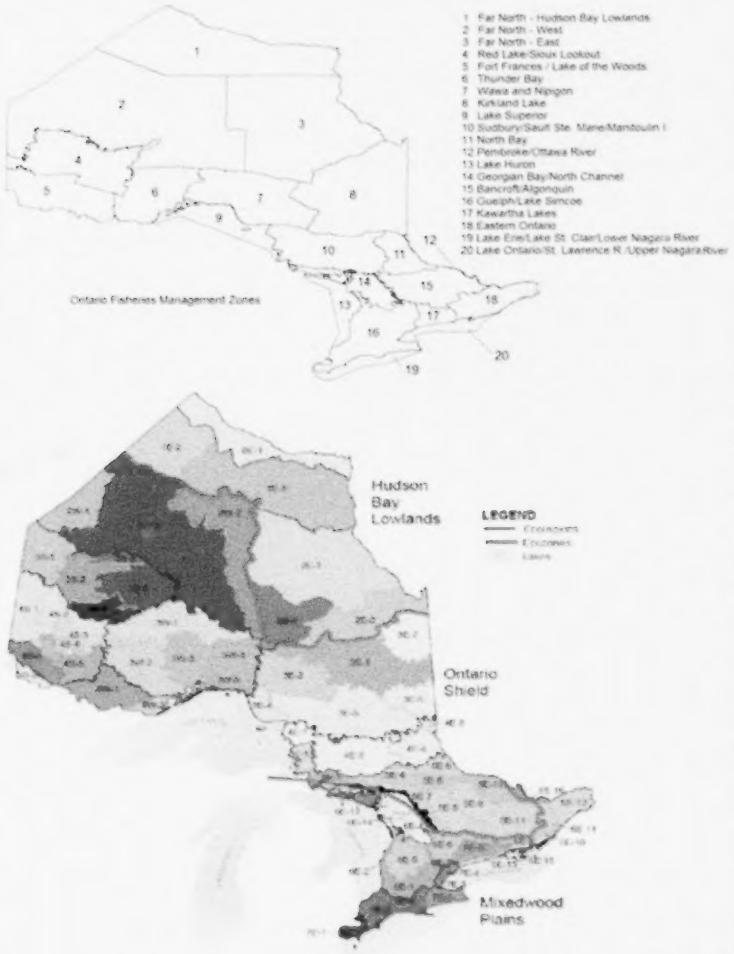


Figure 7. Relationships between the average body-size and the density of fish within a local community in Southern Canada and Europe (open circles), Northern Europe (grey circles) and the Lower Athabasca River tributaries (black circles).

HIERARCHICAL SCALES OF REPORTING CATCH-PER-UNIT-EFFORT

Contributed by Cindy Chu and Dak de Kerckhove, Research Scientists at the Ontario Ministry of Natural Resources and Forestry

In the mid-2000s, the Ontario Ministry of Natural Resources and Forestry shifted from managing provincial lakes individually to a landscape model in which 20 areas (including the Great Lakes) were delineated as Fisheries Management Zones (FMZ; Figure 8). The concept behind this shift was to move the management question from "how is my lake doing?" to "how is my zone doing?". This shift resulted from the recognition that Ontario's recreational fisheries are mobile with changes in stock status and accessibility modifying angling effort across the landscape. Management at the zone level does not preclude attention being given to individual lakes that have a particular management issue, but in general, thousands of lakes across a zone are managed as a whole. Although delineation of the FMZ boundaries was not conducted following an ecologically-based management analysis (e.g. clustering ecological indicators), they were created by experts who took into consideration the watershed, jurisdictional, and terrestrial ecozone and ecoregion boundaries, as well as areas of high activity within the recreational fishery sector. Therefore, the FMZ boundaries do not line up perfectly with terrestrial ecoregion boundaries, but they are in the same general area, and of the same general size (Figure 8). Lakes within FMZs are monitored at the zone level through the Broad-scale Monitoring (BsM) program in which a random selection of lakes from different size classes are sampled, some on a 5 year cycle, to reveal the status of lake fisheries and ecosystems within a zone.



The BsM program presents a challenge in determining how to appropriately report the status of a zone based on the aggregated status of the individual lakes. The challenge falls into two main parts: 1) the more conventional challenge of monitoring enough lakes to obtain a suitable sample size to attain a reasonable level of statistical confidence in the representative indicators, and 2) the less discussed challenge of determining whether the delineation of the zones accurately reflect a similarity of values within the boundaries, and a dissimilarity of values across boundaries. The former challenge is addressed through the implementation of the BsM program, which has become one of the largest lake monitoring programs on the planet with the broadest collection of ecosystem and fisheries data. The latter challenge is less examined in the ecological literature, and will be addressed here.

Figure 8. The Ontario Fisheries Management Zones (Top) and the Ontario Ecozones (red boundaries), Ecoregions (black boundaries) and ecoprovinces (different shades) (Bottom).

The Catch-Per-Unit-Effort (CPUE) of fish from stratified indexed gill netting programs has long been a useful indicator of the standing stock biomass. Biomass and abundance are themselves considered good indicators of fish productivity (de Kerckhove 2014), especially if Production to Biomass ratios are known. The question here is whether the average CPUE reported in a zone is a good representative of the actual status of lake fisheries within a zone. We explore this question in two ways and report our results in Figure 9. First, if FMZs retain a level of homogeneity because they are derived from ecoregions and watershed boundaries, we might expect that CPUEs are fairly consistent across one zone, and different among zones. Chu and colleagues (2016) had already explored this question to some degree by finding that the CPUE from large mesh nets were good ecological indicators within the province and were strongly influenced by climate, total dissolved solids and angling pressure. As we know that at least one of these three variables should change from zone to zone due to changes in latitude, position

relative to the Canadian Shield, and distance from populated centers, we should expect that changes in CPUE from zone to zone will be predictable. To explore this question further, we report the average CPUE for lakes within quaternary and tertiary watersheds, and within FMZs. We certainly found that CPUE varied depending on the spatial scale it was reported at, however, in comparing the average values among watersheds or FMZs, we see a fairly consistent pattern across scales from high catches in the northwest that diminish towards the southeast (Figure 9A-C). Further, it appears that the difference in average values reported among FMZs within the northwest (e.g., see FMZs 2, 4, 5, 6) or the southeast (see FMZs 15, 16, 17, 18) are representative of both the quaternary and tertiary watersheds, which indicates that the FMZ boundaries are indeed partitioning dissimilarities among aquatic resources.

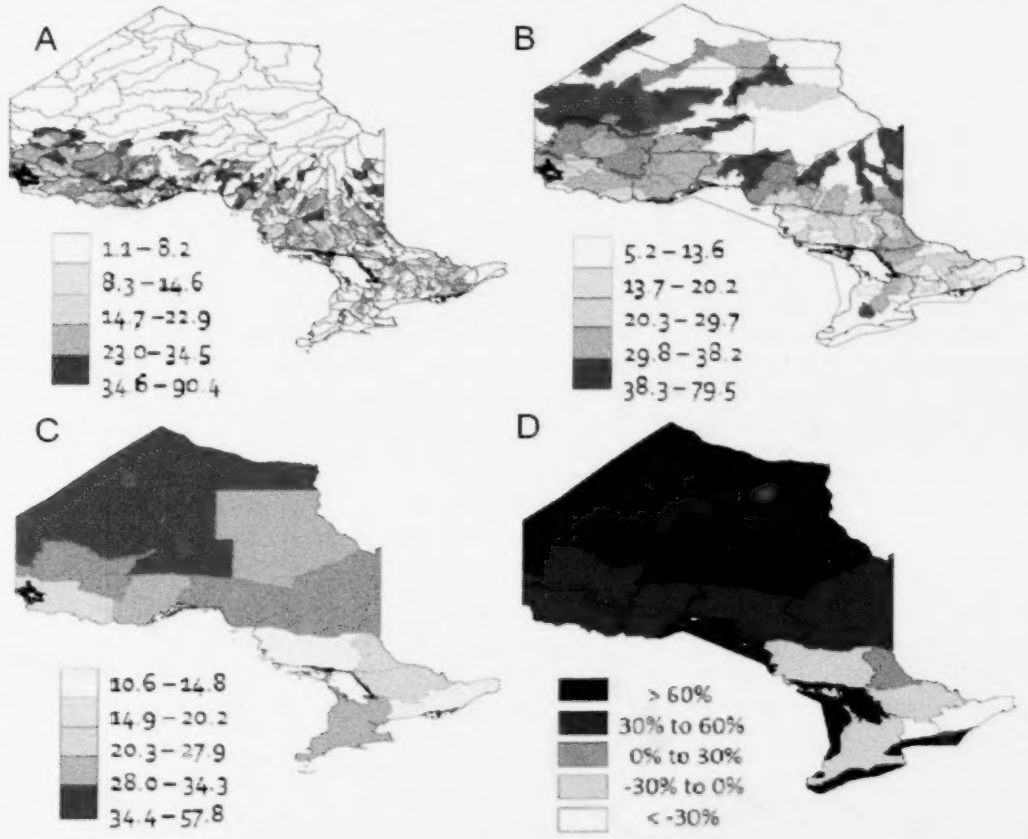


Figure 9. The lake Catch-Per-Unit-Effort of fish reported within quaternary (A) and tertiary (B) watersheds, and within FMZs (C). The percentage of overall fish production remaining in lakes within FMZs following the recreational fishery (D).

Our second approach to testing whether the CPUEs reported for the FMZs are reasonable representations of the status of lake fish productivity within the zones was to compare our observed CPUEs to theoretical expectations of FMZ fish productivity. De Kerckhove and colleagues (2015) developed a landscape lake fishery productivity model for Ontario FMZs in which 1) a climatic-morpho-edaphic index is used to estimate the sustainable yields for the range of lakes found within tertiary watersheds, 2) the yields are converted to productivity and summed / apportioned up to the FMZ level, and 3) the harvest and hooking mortality from catch-

only fisheries are subtracted from the available annual production for each FMZ. The remaining percentage of available fish productivity is reported (see Figure 9D) and can be compared to the standing stock biomass estimated from the BsM CPUEs with the assumption that areas with low (or high) available production remaining after the harvest will contain less (or more) fish and therefore correspondingly low (or high) CPUEs. Our results show the same distinctive decrease in available production from the north to the southeast that we observe in the CPUE. While our theoretical model does not show the same variation in productivity within a particular latitude as the CPUEs, the match is formidable, especially considering that in the absence of the fishery, productivity and catch should generally increase towards the southern regions (as described in the previous contributions).

A BOTTOM-UP APPROACH TO SETTING MANAGEMENT AREAS

Contributed by Ken Minns, Professor Emeritus at the University of Toronto

Setting spatial management units may require different approaches for lentic and lotic fisheries, as well as anadromous versus non-anadromous species. To maximize the amount of fisheries production data available in defined and self-contained aquatic ecosystems and fish stocks, an initial focus on non-anadromous fish in lakes would be a suitable first approach. Within this approach, there are three components to consider: 1) the designation of practical spatial units for establishing benchmarks for fish production, 2) identification of which predictive models currently exist, and 3) how fish production is to be estimated in project-specific locations.

The designation of spatial units should be informed by both the existing frameworks of spatial delineation and the ways in which the spatial units and their attributes might usefully inform the estimation of fish production. An inventory of lakes in Canada has already been started (Minns et al 2008) and is reported by lake size class and secondary watershed. This inventory also reports useful parameters such as mean and maximum depths, Secchi depth, pH and total dissolved solids, which can be used for fisheries production modelling. Overlain on this inventory of lakes is a national picture of environmental and anthropogenic stress (Chu et al. 2003, 2015), which provides the necessary context to explain or potentially correct fish production estimates (e.g. Minns 2009, de Kerckhove et al. 2015). In these latter models, production and environmental stress are predicted at the scale of tertiary watershed and only then apportioned up to broader scales for reporting.

There is a great range of fisheries production models that have been successfully used in North America to relate aquatic habitat size and quality to fish density and production (reviewed in de Kerckhove et al. 2008, Minns et al 2011). Three general types of models may be considered initially: Empirical, Primary Production-Tropho-Dynamics, and Direct. There are few extant empirical models for estimating fish production from relatively simple or easily obtained input variables. The morpho-edaphic index (Ryder et al 1974) is a good example and there are derivatives of that approach which draw on alternate or additional variables (total phosphorus, chlorophyll *a*, mean annual air temperature, etc.). Such models are typically generated from limited scattered data points and likely have low utility for site- or project-specific applications. Primary Production-Tropho-Dynamics models are a broad approach that could involve scaling up from primary production estimates to fish production. This approach has been successfully done in rivers (McGarvey et al. 2010), lakes (Deines et al. 2015), and oceans (Pauly and Christensen). Terrestrial primary production can be estimated from satellite data and strongly influences aquatic productivity. For example, Lewis's (2011) approach allows estimation of net algal primary production in specific lakes using relatively few inputs (total phosphorus, dissolve oxygen, Secchi Depth, lake morphometry, climate metrics). Drawing on Vander Zanden et al (2011) and Vadeboncoeur et al (2003), the Lewis approach could be expanded to macrophytes and epiphytes. Basic Ecopath representations can be generated from the ground up if simple

food webs including key fishery species are specified and assumptions about bioenergetic proportions made (e.g. Walters et al. 2008 for fisheries dynamics; Hossain et al. 2012 ecosystem model for Hamilton Harbour Lake Ontario). This approach overlaps with the recent focus on size-spectrum indicators for monitoring fisheries in Ontario (Giacomini et al. 2016).

The Direct type of methodology impinges on the third component (i.e. the measurement of fish production at a project specific level). Rather than expecting proponents to undertake the long and potentially complex task of having to measure fish production to assess net change or for offsetting, it may be better to parse the problem into two parts using the relationship:

$$Production_{Estimated} = \left(\frac{Production}{Biomass}\right)_{Theoretical} * Biomass_{Observed}$$

In this approach, fish production is estimated from the observed biomass at a particular site multiplied by the theoretical production-biomass ratio. It is not unreasonable to expect proponents to be able to make estimates of abundance/biomass in the lakes they impact or manipulate using standardized netting programs, hydro-acoustic surveys, or electrofishing (nor in streams in which there are well established methods for estimating abundance). This leaves the challenge of how to get P: B values. Randall and Minns (2000) developed an approach for species-specific values and applied it (2002). Their approach did not address the problem of how P:B might vary across the geographic range and across ranges of habitats (large vs small, deep vs shallow etc.), however, there is much recent work in Canada that lays the groundwork to examine how life history parameters that drive these ratios vary in key fish species (Lake Trout, Walleye, Yellow Perch, Cisco, Smallmouth Bass, etc.). Given some simplifying assumptions P: B values might be also estimated from basic via steady-state population calculations (see previous sections in this document). The approach could be extended to a wider range of species and to account for trophic structure issues influenced by biogeography, lake characteristics, and exploitation. Once several species have been assessed there will likely be general patterns which make it easier to extend from fishery species to all in the lakes. A useful demonstration piece of this approach would be to take recent work on fish biomass in Arctic lakes (Samarasin et al. 2015) and P: B ratios from small Ontario lakes (Kelso and Johnson 1991) to estimate fish production in Arctic lakes.

CONCLUSION AND SYNTHESIS

As identifying appropriate spatial units is one of the most challenging aspects of ecosystem classification (Brenden et al. 2008), it will also be a challenge in setting fisheries management areas for the Fisheries Protection Program. It is likely that given the varied types of landscapes across Canada, there will not be one unit of size which will work well enough to be applied indiscriminately. Instead, certain environmental variables will create homogenous regions which vary in size across the country (e.g. watershed sizes). While it is accepted that no boundary type will be universal (Bailey 1987, Loveland and Merchant 2004), there is a large body of evidence that the same factors that drive ecosystem classification (e.g. climatic, physiographic, and other abiotic and biotic factors) also determine regional levels of fish productivity. From the perspective of the implementation of the *Fisheries Act*, where the risk to fisheries productivity remains the central property being assessed, the fundamental question is "what type of ecosystem classification balances broad-scale management with the ability to derive benchmark estimates of fisheries productivity?" Our review offers some insights towards this question. In this synthesis we describe four main insights:

1. Any Ecological Based Management Area approach would increase the number of management zones in Canada from the existing six DFO Administrative Regions.

2. The size of an Ecoregion (~ 20,000 km2) has been demonstrated in our literature review and contributions to be an effective spatial unit for classifying regions with differing water quality and fisheries resources. This type of approach would lead to a high number of management units across the country (for example, note that there are 194 terrestrial Ecoregions in Canada).
3. Our reviews suggest that any classification scheme that addresses fisheries production should include at least one variable from each a terrestrial, aquatic and anthropogenic mechanism. We also note that these variables do not necessarily need to be chosen to act at the same spatial scale.
4. We recommend that a classification scheme can be hierarchical, with the broadest spatial scale delineating climatic or geological processes, and subsequently more refined spatial scales include place-dependent or -independent mechanisms that can be used to estimate fish production across the management area (e.g. fish production determined by lake size could be summed for all lakes within a management area).

First, it is clear that any existing ecological classification system will result in more management areas than currently exist under DFO's framework. For example, assuming the fifteen terrestrial Ecozones in Canada provided reasonable enough boundaries for fisheries management (as the Ecoregions seem to do in Ontario and British Columbia), switching to an EBMA approach to managing fisheries productivity across the country would add nine management areas to the existing six DFO management regions at the broadest level of classification. In this hypothetical scenario, the existing Pacific region would remain relatively self-contained in four Ecozones, while the Gulf and Maritime regions would be amalgamated into one Ecozone. Due to the effect of the Canadian Shield, the existing boundaries between the Quebec region and the Central and Arctic region, as well as between the Quebec and the Newfoundland and Labrador region, would not be ecologically relevant. And of course, the Central and Arctic region itself would be partitioned into nine Ecozones that better represent the local conditions on the Canadian Shield, the James Bay lowlands, northern and southern prairies and grasslands, boreal forest, tundra and the far north Arctic Archipelago. If instead the freshwater Ecozones (Abell et al. 2008) were used as the most reasonable management structure, due to their similar size and number to the terrestrial Ecozones, the boundaries would be slightly different because watersheds are taken into account, but the general split of the existing regions would remain the same. Note that it isn't clear that the freshwater Ecozones would provide a better management unit than their terrestrial equivalent. At such a broad spatial scale the boundaries that watersheds provide are clearly importation from a biodiversity perspective due to natural breaks in species ranges but not necessarily from the perspective of fish productivity which can be driven at large scales by processes that cross watersheds (i.e. geology and climate). The very simple hypothetical approach we present here (i.e., that of using the existing broadest scale Ecozones as fisheries management areas) is appealing in that the regions seem broad enough to be logistically convenient, and likely a few of the ecoregions can be still be effectively administered by one office, but given a scenario in which the benchmark fisheries productivity is needed, it is not clear that they are fine enough to capture the variation in productivity within each region.

Second, the broadest spatial scale of ecological classification that has been demonstrated to effectively partition the variation in aquatic parameters that are relevant to fisheries productivity among regions is at a size of around 20,000 km^2, which is equivalent to the Ecoregion scale of classification and up to two orders of magnitude smaller than the Ecozones. Cheruvilil and colleagues (2008, 2013) found that this spatial scale best explained variation in lake water chemistry including Total Phosphorus which is a key driver of fisheries productivity. Dr. Mark Hoyer's contribution argued that the United States' EPA Level III Ecoregions were effective at partitioning Secchi depth, which is a key driver of species distributions but also particularly of Walleye abundance in Canada. While much of Dr. Hoyer's work focused on Florida, the same

general patterns were found closer to Canada in the Upper Midwest of the United States (Lottig et al. 2014). Kyle Wilson's contribution demonstrated that despite the important effects of elevation on fisheries productivity, British Columbia is divided into 8 Management Regions with defined boundaries, each of which encompasses the variation from elevation. Drs. Cindy Chu and Dak de Kerckhove presented catch data from Ontario's Fisheries Management Zones which divide the province's landmass into roughly 14 areas which are each the size of an Ecoregion. Assuming that the Ecoregion size is therefore an effective spatial unit of fisheries productivity, using Canada's existing terrestrial Ecoregions would divide the country into 194 terrestrial management units, of which many in prairie, grassland and tundra ecosystems can be much smaller than the areas demonstrated in British Columbia and Ontario to be effective sizes for managing fisheries.

Third, in developing classification schemes, our review (including Melles et al. 2013 extensive review on Aquatic Ecosystem Classification), suggests that environmental variables that effectively partition variation among regions are not often shared across scales (see Figure 3.4 in their report) however, the class of variable which drives aquatic conditions can remain important. For example, in Firman and colleagues (2010), land-use had a strong influence on fish density regardless of whether this class of variable was expressed as road density at broad scales or cow density at fine scales. This consistency in the class of a variable is confirmed by Leach and Heron (1992) who suggest that temperature, area, nutrient levels and lake morphometry are important variables at global, regional and infra-regional scales. All four of those variables can be expressed at broad and fine scale parameters (e.g. ambient temperature can be affected by climatic regimes at broad scales or groundwater springs at fine scales). As demonstrated by Cheruvilil and colleagues (2013), if a new classification scheme was developed to be tailored to the implementation of the *Fisheries Act*, incorporating at least a terrestrial, aquatic and anthropogenic variable would likely be valuable.

Last, given the wide range of predictive models available for fisheries scientists (Minns et al 2011), it appears that fish distributions, abundance and production can be predicted using habitat based correlates at either broad spatial scales for which the data is largely available (e.g. Minns et al. 2009) or data that is relatively simple to collect at finer scales. From a management perspective, the metric identified by Bailey (1983) that "habitats within a management region will all respond similarly to management actions" is important to evaluate. For some organisms it is more likely a place-independent type management plan could be more effective than regional management. For example, Brook Trout might benefit more from conservation efforts that target headwater environments across many management areas. For another example, Lake Trout might benefit more from management plans that target particular lake size classes rather than management areas (Shuter et al. 1989). For physiographically complex geographic regions (e.g., British Columbia), contiguous regions may poorly characterize the biogeoclimatic variation driven by changes in latitude, longitude (e.g., coastal or mountain effects), or elevation which would lead to differences in fish productivity and social-ecological behaviour. In such circumstances, place-independent management that targets waterbody size/area, alpine headwaters, alpine lakes may more appropriately capture the variation in productivity or biomass metrics.

A greater degree of effectiveness at one type of approach does not necessarily preclude the other approach from being valuable. Regional management plans appear to be working well in Ontario for Lake Trout, where catch restrictions show positive benefits in restoring overfished populations across many lake size classes. Many of the models presented in this report use fine scaled data (e.g. lake area or reach-level fish habitat maps) which are then aggregated to be reported or further manipulated at a higher spatial scale (e.g. tertiary or secondary watersheds; Minns 2009, Total E&P Canada 2014, de Kerckhove et al. 2015). This approach suggests that a tiered approach, much like that suggested by the Hawkins and Norris (2000) symposium, could

be a promising route to developing fisheries productivity benchmarks. Hawkins and colleagues (2000) concluded that local habitat features are the foundation of a classification scheme, and that larger-scale features are used for refinement. In a fisheries production model, we may find instead that the reverse is true, and that it is the large-scale features that drive fundamental relationships between temperature and nutrient availability that set the foundation of the scheme, and that the finer scale features are those that are used for refinement. This conceptual framework would match a growing consensus that the creation of effective Ecologically Based Management Areas uses a mixture of top-down regional approaches, and bottom-up methods that include clear mechanisms between landscape features and biotic metrics (Wichert et al. 2004, Seelbach et al. 2006) leading to hierarchical schemes in which larger spatial scales have contiguous regions and lower scales are non-contiguous or even overlapping. The practical application of this approach would be to include top-down regional approaches that are known to influence fish production, and provide a useful boundary among regions. Climate and changes in geology appear to be good candidates for creating these regions, as do the existing Terrestrial Ecozones or Ecoregions as a reasonable template. At lower scales, habitat and anthropogenic mechanisms will primarily drive fish production in place-independent relationships. However, when a management decision needs to be made, these fine-scaled associations can be used to determine levels of fish productivity across the management unit (as done in de Kerckhove et al. 2015 in Ontario).

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